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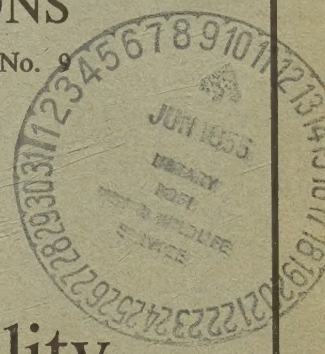

Estimation of Growth and Mortality in Commercial Fish Populations

BY

J. A. GULLAND, B.A.

Naturalist on the Staff of the Ministry of Agriculture and Fisheries

LONDON: HER MAJESTY'S STATIONERY OFFICE

1955

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Estimation of Growth and Mortality in Commercial Fish Populations

INTRODUCTION

the study of the dynamics of any fish population, particularly in relation to its behaviour under ploitation by man, there are a number of parameters which must be determined. Among these firstly the population density and its age and size composition, and following naturally from se, the growth rate of the fish, the mortality rate, split up if possible into that due to fishing, d that due to other causes, and the comparative strength of year-classes. All of these can be aluated by an examination and study of the commercial landings, at least when the commercial tistics are sufficiently detailed, provided that the age of the fish can be determined fairly accurately. is has, of course, been done regularly for many different species of fish in a large number of untries, but the methods used have usually lacked any statistical evaluation of variance and ssible bias. The present paper attempts to analyse the procedure of market sampling and the bsequent analysis from a mathematical and statistical viewpoint. The ultimate object will be obtain the best estimates of the parameters outlined above. Usually there are a large number methods by which the data can be collected and interpreted, giving a number of different imates. The 'best' estimates will be those which, in statistical terms, are unbiased and of nimum variance. These terms may be explained most easily by comparison with a gun shooting a target. If the gun is biased the shots will all tend to go to one side. In the hands of a skilled n, the shots will be tightly bunched on the target, with little scatter, or variance ; with a poor ot they will have a large scatter or variance. Thus, if the shots are unbiased and of small variance y will all be tightly bunched round the bull's-eye; if biased and of small variance they will l be in a bunch, but to one side of the target ; if unbiased but with large variance they will widely scattered, but their average position will be in the centre of the target. In this work, ich may be compared to estimating the position of the bull from the known position of the shots, unbiased estimate is normally more useful than one that is of smaller variance, but is biased. ile a large variance will soon show up in the discrepancy between separate estimates, a large s cannot be detected in this way.

For an unbiased estimate, the variance gives an exact measure of the accuracy—the smaller variance the greater the accuracy. Thus, the estimate with the minimum variance is the one ing the greatest accuracy for a given amount of effort ; or from a different viewpoint, it is estimate which will have a desired accuracy with the least possible effort.

The study of a natural population from the commercial landings is best considered as a two-ge process ; as the sampling of a sample. The sampling of the landings is a reasonably simple istical problem, wherein most of the processes can be directly controlled. This will be dealt h in Part I which deals with the direct sampling for length and the sampling for age distributions. commercial landings are only a sample from the whole natural population and a sample that btained in a far from random manner. Part II will describe how a knowledge of the com-cial landings can give a knowledge of the composition of the true natural population. Part III describe how a knowledge of this can be used to give, as far as possible, accurate and unbiased mates of the parameters of growth and mortality of the natural population. Within each ion theoretical methods will be developed first, which will be then applied to the North Sea ce and to other species.

PART I

ANALYSIS OF SAMPLES FROM COMMERCIAL LANDINGS

Length distribution of landings

The sampling of the landings is a straightforward statistical problem and can be dealt with by normal statistical techniques. Briefly, the problem is to estimate the actual numbers landed in each age, or length, group, and to do this with the smallest variance on the estimates. The population—in the statistical sense—is exactly defined and it is theoretically possible to find the age and length of every fish landed—or even practically possible for sufficiently rare fish.

In England the measurements are made immediately after the fish are landed from the ships when they are laid in boxes on the market before being auctioned. The more important species are usually sorted into two or more size categories, and this sorting can be of great assistance in increasing the accuracy of the estimates of length distribution. However, we will deal at first with only one category landed. The measuring technique consists of measuring samples of fish (the lengths being the total length, recorded to the cm. below) from a number of randomly selected ships. The quantity of fish measured from each ship is the same, but the size of this sample, and the number of ships from which samples are taken, are variable, and the efficiency of the sampling technique is determined critically by these factors. As the total weight of fish landed can be known, the figure for which an estimate is needed may be considered to be the average number Λ of fish of a certain length-group in a fixed weight, e.g., a ten-stone box. The following statistical analysis will determine the variance of the estimate of Λ and how it is influenced by the number and size of samples.

Let n = number of ships from which samples are taken.
m = average number of fish in each sample.
W_i = weight landed from i^{th} ship. $i = 1, 2, 3 \ldots\ldots n.$
λ_i = true mean number per unit weight of a particular length-group in i^{th} ship.
l_i = estimated mean number per unit weight of a particular length-group in i^{th} ship.
L = estimated mean number per unit weight of a particular length-group in total landings.

$\therefore$ From these definitions it follows that total number of fish landed in a length-group from the n ships =

$$\sum_{i=1}^{n} W_i \lambda_i$$

And estimated number of fish landed in a length-group from the n ships =

$$\sum_{i=1}^{n} W_i l_i$$

$$\text{and } \Lambda = \frac{\sum W_i \lambda_i}{\sum W_i} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1.1)$$

$$L = \frac{\sum W_i l_i}{\sum W_i} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1.2)$$

It is possible and sometimes convenient to take weighting coefficients other than W, and in particular to take as an estimate for Λ, $L' = \frac{1}{n} \sum l_i$. This is often easier to compute but will give a biased result if there is a correlation between the size of catch and length distribution.

Equation (1.2) can be rewritten in the form

$$L \sum W_i = \sum W_i l_i$$
$$= \sum W_i \Lambda - \sum W_i (\Lambda - \lambda_i) - \sum W_i (\lambda_i - l_i) \quad \ldots\ldots\ldots\ldots (1.3)$$

ow $\lambda_i - l_i$ is the sampling error on the i^{th} boat and $\Lambda - \lambda_i$ is the difference of the i^{th} boat from e mean. These terms will be approximately independent.

$$\therefore \left(\sum W_i\right)^2 var\ L = \sum var \left\{ W_i(\Lambda - \lambda_i) \right\} + \sum W_i^2\ var\ (\lambda_i - l_i) \ldots\ldots (1.4)$$

Now assume at first that $var\ (\Lambda - \lambda_i) = \sigma_1^2 =$ constant independent of i.

Also, if λ_i does not vary over too great a range, $var\ (\lambda_i - l_i)$ will be nearly constant and inversely oportional to the number of fish in each sample ; i.e. $var\ (\lambda_i - l_i) = \frac{1}{m}\sigma_2^2$

$$\therefore \text{from (1.4), } var\ L = \frac{\Sigma\ W_i^2}{(\Sigma\ W_i)^2}\left(\sigma_1^2 + \frac{1}{m}\sigma_2^2\right)$$

Now, let $\sigma_2^2 = \alpha\ \sigma_1^2$ and $mn = N =$ number of fish measured.

$$\therefore var\ L = \frac{\Sigma\ W_i^2}{(\Sigma\ W_i)^2}\left(\sigma_1^2 + \frac{1}{m}\alpha\ \sigma_1^2\right)$$

$$= \frac{\Sigma\ W_i^2}{(\Sigma\ W_i)^2}\frac{\sigma_1^2}{m}(m + \alpha) \quad \ldots\ldots\ldots\ldots\ldots\ldots (1.5)$$

the W_i's are nearly equal, then $\frac{\Sigma\ W_i^2}{(\Sigma\ W_i)^2}$ will be nearly equal to $\frac{1}{n}$; in fact it will be rather larger, pending on the variance of the W_i's but to a fair approximation,

$$var\ L = \frac{1}{n} \cdot \frac{\sigma_1^2}{m}(m + \alpha)$$

$$= \frac{\sigma_1^2}{N}(m + \alpha) \quad \ldots\ldots\ldots\ldots\ldots\ldots (1.6)$$

this expression σ_1^2 and α are constant, but N and m can be varied.

Assuming that m and N can be varied independently, then for a fixed number of measurements, ie minimum variance is achieved when m is least, viz. $= 1$.

$$\text{and } (var\ L)_{min} = \frac{\sigma_1^2}{N}(1 + \alpha) \quad \ldots\ldots\ldots\ldots\ldots\ldots (1.7)$$

nd the "efficiency" of any other sampling pattern can be defined as

$$\text{Efficiency} = \frac{(var\ L)_{min}}{var\ L} = \frac{1 + \alpha}{m + \alpha} \quad \ldots\ldots\ldots\ldots\ldots\ldots (1.8)$$

In practice, because it takes an appreciable time to move the measuring board and other quipment from one ship to another, the taking of very small samples from a large number of ips will reduce the number of fish that can be measured in a given time and the least value of *r* L for a given amount of sampling effort is found by substituting into (1.6) in the form

$$var\ L = \sigma_1^2\left(\frac{1}{n} + \frac{\alpha}{N}\right) \quad \ldots\ldots\ldots\ldots\ldots\ldots (1.9)$$

e values of n and N for different sampling patterns. When $m = \alpha$ then the two terms in (1.9) e equal. If $m > \alpha$ the dominant term in (1.9) is $\frac{\sigma_1^2}{n}$ and this will not be reduced by increasing m.

The above work is referring throughout to the number of fish of a certain size in a given weight, ually a box, and therefore the weight of the sample must be known. This means that the sample usually a whole number of boxes, though sometimes if there are many fish in a box only part e measured. The rest of the fish must be counted or weighed to determine what fraction of e box has been measured.

The variance of $l_i\left(= \sigma_1^2 + \frac{1}{m}\sigma_2^2\right)$ can be determined at once from any set of routine samples. and σ_2^2 are determined separately and hence α found, by taking two separate samples of the me size from each ship. An analysis of variance is done in the usual manner as indicated below.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Within Ships	n	A	$\frac{1}{n} A$
Between Ships	$n-1$	B	$\frac{1}{n-1} B$
Total	$2n-1$	C	

Denoting the two values of l from the i^{th} ship by l_i, l_i'

then C = total sum of squares =

$$\sum_{i=1}^{n} \left\{ (L - l_i)^2 + (L - l_i')^2 \right\}$$

A = "within ship" sum of squares =

$$\sum_{i=1}^{n} \tfrac{1}{2} (l_i - l_i')^2$$

B = "between ship" sum of squares =

$$\sum_{i=1}^{n} 2 \left\{ L - \tfrac{1}{2} (l_i + l_i') \right\}^2$$

and $A + B = C$

Now also Expectation of $A = \text{n} \cdot \frac{1}{m} \cdot \sigma_2^2$ .....(1.10)

Expectation of $B = 2(n-1)\left(\sigma_1^2 + \frac{1}{2m}\sigma_2^2\right)$ .....(1.11)

Expectation of $C = 2(n-1)\sigma_1^2 + \frac{2n-1}{m}\sigma_2^2$ .....(1.12)

and therefore estimates of σ_1^2 and σ_2^2 are

$$\frac{1}{m}\sigma_2^2 = \frac{1}{n} A \quad \text{.....(1.13)}$$

$$2\sigma_1^2 = \frac{1}{n-1} B - \frac{1}{n} A \quad \text{.....(1.14)}$$

and hence $\alpha = \frac{\sigma_2^2}{\sigma_1^2} = \frac{\frac{m}{n} \cdot A}{2\left(\frac{1}{n-1} B - \frac{1}{n} A\right)}$ .....(1.15)

If we assume that the sampling from a single ship is described adequately by the binomia distribution, then a theoretical value for $\frac{1}{m}\sigma_2^2$ can be found at once, for $\frac{1}{m}\sigma_2^2 = \frac{1}{m}\lambda_i (k - \lambda_i)$ where

k = total number of fish in unit weight.
λ_l = number of fish of required length.

var $l_l = \sigma_1^2 + \frac{1}{m}\sigma_2^2$ is found by the usual methods and hence σ_1^2, σ_2^2 and α can be evaluated separately.

So far, only one particular length-group has been dealt with ; of course the same calculation can be done for each length-group and the variances of each estimate calculated. For each group there will be a sampling design giving the minimum variance, but though there is no *a priori* reason for these designs being the same for all length-groups, usually there will be a compromise scheme which will be reasonably efficient, for at least all the more important lengths. These calculations are enough to determine the most efficient sampling design for a given amount of effort, but the absolute amount of sampling required is less easy to state, though some criteria will be suggested

later in this paper. In practice, the amount of sampling it is physically possible to do is usually well below any theoretical upper limit of what is desirable.

Most of the plaice caught by English trawlers in the North Sea are landed at the two ports of Grimsby and Lowestoft, and routine measurements are carried out at both. The fish are landed in ten stone boxes and are usually sorted into three main categories, Large, Medium and Small, with sometimes two other minor categories, Rough and Slabs. These last make up only a very small part of the total landings, but the Slabs contain a considerable part of the very large and old fish, so that if they were neglected there would be a noticeable under-estimate of the numbers of old fish. To find the values of σ_1^2 and σ_2^2 two boxes of each main category were measured from a number of different ships in October 1951 and an analysis of variance carried out. Table 1.1 shows this for three separate 5 cm. length-groups, for the number of fish of that length in 50 fish sorted as Medium.

TABLE 1.1

Analysis of variance of plaice measurements

Source of Variation	D.F.	Length Group					
		30–34 cm.		35–39 cm.		40–44 cm.	
		Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.
Within Ships	12	141·0	11·75	145·0	12·08	62·5	5·21
Between Ships	11	965·5	87·77	622·8	56·62	88·5	8·04
Total	23	1106·5		767·8		151·0	
Mean Number		18·75		28·08		3·04	
Expected Variance		11·72		12·31		2·86	

For the 35–39 cm. group then, we have in our notation—

$$145 = A = n \cdot \frac{1}{m} \cdot \sigma_2^2 = 12 \cdot \frac{1}{50} \cdot \sigma_2^2$$

$$622{\cdot}8 = B = 2(n-1)\left(\sigma_1^2 + \frac{1}{2m}\sigma_2^2\right) = 2.11 \cdot \left(\sigma_1^2 + \frac{1}{100}\sigma_2^2\right)$$

$$\therefore \quad \sigma_2^2 = 50 \cdot 12{\cdot}08 = 604$$

$$\sigma_1^2 = 28{\cdot}31 - 6{\cdot}04 = 22{\cdot}27$$

$$\alpha = 27{\cdot}12$$

Strictly, tests of significance cannot be carried out on this analysis, as the numbers are not distributed exactly normally ; however, the difference is probably not very great and on the assumption of normality the differences between the mean squares between ships and within ships is highly significant for the 30–34 cm. group ($P < \cdot001$) and for the 35–39 cm. ($P \simeq \cdot01$). The average number of each length is also given in Table 1.1 and from this it is possible to calculate what the variance would be assuming random sampling from a uniform population. If the average number $= n$, then the theoretical variance for a sample of 50 fish is $\frac{n \times (50 - n)}{50}$; and this is given in the last row of Table 1.1. For each length-group this figure is very similar to the within-ships mean square, and it is reasonable to suppose that the main contribution to this mean square is the error of random sampling. The value of α has been calculated from the 35–39 cm. group and is 27·12 and similar calculations give $\alpha = 15{\cdot}46$ and $\alpha = 184{\cdot}1$ for the 30–34 cm. and 40–44 cm. groups respectively. This shows that taking samples of more than 15 (for the 30–34 cm. group) or 30 (for the 35–39 cm. group) will not greatly increase the accuracy of the result, as we have shown earlier that the accuracy can only be significantly increased by taking more samples. This is because there is considerable difference in the size composition of catches of different ships though the catch of any one ship is homogeneous. Thus, a sample of say 20 fish from a ship

will give a very good idea of the proportion of 30–34 cm. group fish in that ship and subsequent samples from the same ship will give very little additional information, while the size composition of the other ships remains unknown. It is desirable therefore to increase the number of samples taken, even at the cost of considerable reduction in the number of fish measured. There are practical difficulties in measuring from a large number of different ships, but in the time normally available for measuring medium plaice, about twenty minutes, two designs which require about the same effort are (A) to measure an entire box = 200 fish from one ship, or (B) to measure 50 fish from each of two ships ; in the notation of (1.9), for the 30–34 cm. group this gives

$$\text{design A} \quad var\ L = \sigma_1^2 \left(\frac{1}{n} + \frac{\alpha}{N}\right)$$
$$= 38{\cdot}01 \left(1 + \frac{15{\cdot}46}{200}\right)$$
$$= 40{\cdot}95$$
$$\text{design B} \quad var\ L = 38{\cdot}01 \left(0{\cdot}5 + \frac{15{\cdot}46}{100}\right)$$
$$= 24{\cdot}88$$

which gives a clear advantage to design B, despite the fact that only half the number of fish were measured. There is also a gain for the 35–39 cm. group—25·29 reduced to 17·17, though a slight loss for the 40–44 cm. group—2·72 increased to 3·31. However, the most abundant, and therefore probably the most important length-groups are those from 30–39 cm. and the improvement in the accuracy of these more than counter-balances the loss on the less important lengths.

There is one big difficulty in increasing the number of samples at the expense of the size of samples, and that is the determination of the actual weight of fish that has been sampled and hence what fraction of the total catch has been sampled. The plaice at Lowestoft are landed in ten stone boxes and thus the weight of a sample of one or more complete boxes is known at once, but generally, a whole box is much bigger than the most desirable size of sample. At present the weight of the measured fraction is determined by counting the remainder of the fish in the box, e.g., if 50 fish are measured and 150 counted, then the weighed sample is $\frac{50}{200} = \frac{1}{4}$ of the total box, i.e. $2\frac{1}{2}$ stone. The counting takes some appreciable time and is one reason why two samples each of 50 fish takes about the same time to carry out as one sample of 200 fish.

The need for such counting can fortunately be reduced by using the mean length of the fish measured. If this average length is plotted against the number of fish in a box there is a very close relationship, which, over the range occurring in practice, is linear ; the smaller the fish the more there are in the box. An example of this is given in Fig. 1.1, calculated for the Small plaice at Lowestoft in March 1953. The number of fish in the box, and hence the proportion measured can be obtained from this graph thus saving an appreciable time on the market. The actual line will vary due to changes in condition in the fish, so that in some samples in each period (e.g. a month) all the fish in the box will have to be counted in order to determine the line. In Fig. 1.1. the regression line is $y = 251{\cdot}5 - 19{\cdot}612\ (x - 31{\cdot}304)$, where y = number of fish in a box, x = average length in centimetres. The scatter of points about the line is fairly small, as is shown by the correlation coefficient of 0·806. The residual variance of the number per box about the line is 175·1, with a standard deviation of $\sqrt{175{\cdot}1} = 13{\cdot}2$. The extra variance due to estimating the total numbers per box given to the number of a given length-group, which forms a fraction p of the total will therefore be $175{\cdot}1 \times p^2$. This is for the length-groups 25–29, 30–34 and 35–39 cm., 26·5, 42·9 and 2·28 respectively ; the observed variances of

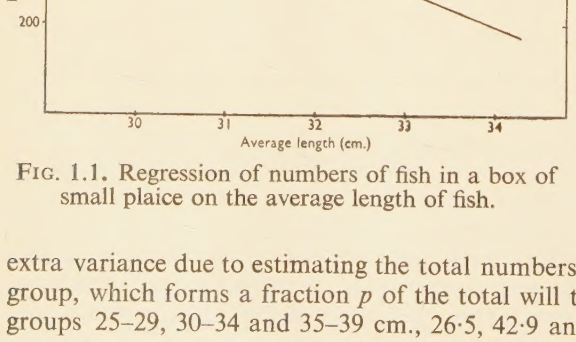

FIG. 1.1. Regression of numbers of fish in a box of small plaice on the average length of fish.

he numbers in these three length-groups are 1953·6, 420·2 and 174·75, and only for the 30–34 cm. ength-group does the additional variance amount to as much as 10 per cent of the whole. The light errors introduced by estimating the number in a box from the length composition of the ample are for this category of plaice therefore so small compared with the other sampling errors hat they can be neglected.

When only part of a box is measured, there is a considerable tendency unconsciously to pick ut a particular size of fish, usually the biggest, and unless this is corrected, a considerable bias s introduced. This type of selection is difficult to eliminate even when one is aware of it, for then, n trying to get a fair proportion of small fish, one is liable to over-correct and take too many. f, instead of picking the fish to measure anywhere off the top, so that it is possible to avoid the maller fish, the sample is consistently taken from one side, then for a sample of about half a box he measurer is forced to take all fish that were originally on that side and personal selection is liminated. This procedure has been adopted at Lowestoft and has been tested at intervals by neasuring the rest of the box after the sample has been measured and there has been no significant difference between the two parts. This bias is different from the digit bias observed by Sette (1941) which occurs when the last figure in a reading (in his case length to the nearest mm.) is difficult o observe, and is not important in the grosser length measurements used in this type of population study.

Beside the plaice, measurements of hake and cod have been made at English ports, and these have shown the same things as the plaice measurements ; little variation within any particular anding, but marked differences between landings. Table 1.2 shows the results of measurements of hake at Fleetwood in 1952 and is given in the same form as Table 1.1. In this case more than two boxes were measured from some ships, involving slight changes in the calculations.

TABLE 1.2

Analysis of variance of hake measurements

Sub-sample size = 1 box = 30 fish

Source of Variation	D.F.	Length Group			
		60–64 cm.		65–69 cm.	
		Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.
Between Ships	14	751·99	53·71	434·72	31·05
Within Ships	29	176·92	6·10	369·17	12·73
Total	43	928·91		803·89	
Variance ratio		8·80		2·44	
		$P < 0·001$		$0·01 < P < 0·05$	

This is based on the measurements of 44 boxes of medium hake, which were averaging about 30 fish to the box ; the big difference between the within ships and between ships mean square is obvious. The value of P, from tables of the variance ratio have been given as a rough guide to the significance of the difference, though the values are not exact because the distributions are some way from being normal.

Tables 1.3 and 1.4 below give some results from measurements of unsorted bulk cod at Grimsby from Regions IIA (Norwegian Coast) and I (Barents Sea and Murman Coast) respectively in the early part of 1952.

TABLE 1.3

Analysis of variance ; Grimsby cod from Region IIA

Sub-sample size = 1 box = 15–20 fish

Source of Variation	D.F.	Length Group					
		60–69 cm.		70–79 cm.		80–89 cm.	
		Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.
Between Ships	5	23·1	4·62	113·7	22·7	9·8	1·96
Within Ships	14	65·5	4·68	114·5	8·2	72·0	5·14
Total	19	88·6		228·2		81·8	
Variance Ratio		0·99		2·78 $0{\cdot}05 < P < 0{\cdot}1$		0·38	

TABLE 1.4

Analysis of variance ; Grimsby cod from Region I

Sub-sample size = 1 box = 20–40 fish

Source of Variation	D.F.	Length Group					
		40–49 cm.		60–69 cm.		80–89 cm.	
		Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.	Sum of Sq.	Mean Sq.
Between Ships	4	363·6	90·9	82·9	20·7	14·5	3·6
Within Ships	12	360·7	30·1	140·7	11·7	23·0	1·9
Total	16	724·3		223·6		37·5	
Variance Ratio		3·02 $0{\cdot}05 < P < 0{\cdot}1$		1·77		1·89	

TABLE 1.5

Analysis of Variance of North Sea Cod landed at North Shields in March, 1952

Category	Source of Variation	D.F.	Length Group													
			40–49 cm.		50–59 cm.		60–69 cm.		70–79 cm.		80–89 cm.		90–99 cm.		100+ cm.	
			S of Sq.	M. Sq.	S of Sq.	M. Sq.	S of Sq.	M. Sq.	S of Sq.	M. Sq.	S of Sq.	M. Sq.	S of Sq.	M. Sq.	S of Sq.	M. Sq.
Selected	Between Ships	8	69·4	8·68	523	65·37	141·78	17·72								
SMALL	Within Ships	9	73·0	8·11	47	5·22	26·00	2·89								
Sub-sample 1 box = 20–35 fish	Total	17	142·4		570		167·78									
	Variance Ratio		1·07		12·52		6·13									
					$P < 0{\cdot}001$		$P < 0{\cdot}01$									
MEDIUM	Between Ships	9			11·05	1·23	172·8	19·20	6·8	0·76	29·8	3·31				
	Within Ships	10			5·50	0·55	35·0	3·50	32·0	3·20	9·0	0·90				
Sub-sample 1 box = 10–15 fish	Total	19			16·55		207·8		38·8		38·8					
	Variance Ratio				2·24		5·49		0·24		3·68					
					$P \simeq 0{\cdot}1$		$P = 0{\cdot}01$				$P < 0{\cdot}05$					
LARGE	Between Ships	11							148·9	13·54	724·2	65·84	60·7	5·52	235·25	21·39
	Within Ships	36							287·0	7·97	1252·8	34·80	255·8	7·10	224·00	6·22
Sub-sample 5 boxes = 30–35 fish	Total	47							435·9		1977·0		316·5		459·25	
	Variance Ratio								1·70		1·89		0·78		3·44	
									$0{\cdot}1 < P < 0{\cdot}2$		$P > 0{\cdot}1$		$P < 0{\cdot}1$		$P < 0{\cdot}01$	

Finally in Table 1.5 the landings of cod from the North Sea at North Shields have been analysed. At this port the fish are sorted into a number of different categories, and the results from three of the categories are shown in the table. Except possibly for the cod from Region IIA, all the results show the same tendency for a much larger variance between ships than within ships, even though the sample sizes are only of from 10 to 40 fish. An interesting feature is that the ratio of the two variances for any category of fish tends to be highest for the central sizes of that category. Thus the benefits in taking more samples, rather than bigger samples, would be greatest for these central sizes, which are the commoner and generally more important sizes.

Though these examples do not give a complete cover of even the English landings, they do show that the principle of taking a large number of small samples is widely applicable, and that the size of sample beyond which it is wasteful of effort to go may be very small, only 10–20 fish.

Stratified Sampling

So far the landings have been treated as a whole ; in reality they are caught at different times, in different places, often by different types of gear and types of ship and, finally, are often sorted into different categories, by size or condition. Some or all of these can be taken into account in the sampling design and the choice of which to use, and also what divisions to take, e.g. whether to divide time of capture into quarters, months, weeks or days, can make a noticeable difference to the final result. These are examples of the general problem of stratified sampling (see Deming 1950) which is of considerable importance in this type of work and will occur again in the problem of age censuses and is therefore worth examining here in detail. For unstratified sampling the population is treated as a whole and the differences are ignored ; all the samples are taken together to give an estimate. For stratified sampling the population is divided into several strata ; each of these is in effect sampled separately and the results for each added together to give an estimate for the whole population. Stratified sampling has the advantage that it can take into account non-uniformity of the population. Against this, samples in one stratum do not give any information on any other stratum. The following calculations will provide a mathematical basis for choosing when to use stratified sampling and what divisions to take. As before we wish to discover a design of sampling which will give an estimate which is unbiased and of minimum variance.

Suppose then there is an aggregate of N fish, say a year's landings, which is divided into k strata, there being N_i fish in the i^{th} strata and we wish to determine the proportion, π, of the fish of a certain type, e.g., of a particular length, in the population, where π_i = the proportion of the type in the i^{th} strata. The division may be of many types, e.g. time of landing, method of capture, market category, etc. A stratified sampling procedure (design A), would be to take a total of n fish, n_i being taken at random and independently in the i^{th} strata where $\sum n_i = n$. Alternatively, these n fish could be taken independently and randomly from the whole population (design B).

Let $n_i p_i$ = number of fish of given type in sample from i^{th} strata (design A).

np = number of fish of given type in total sample of design B

Expectation of p_i $= \pi_i$

and Expectation of p $= \pi$

Let $var\ p_i$ $= \dfrac{1}{n_i}\,\sigma_i^2$

and $var\ p$ $= \sigma_B^2$

and with design A, the estimate of π, the proportion in the whole population is—

$$p_A = \frac{1}{N} \sum N_i p_i$$

$$\therefore \text{ Expectation of } p_A = \frac{1}{N} \sum N_i \pi_i = \pi$$

$$\text{Variance of } p_A = \frac{1}{N^2} \sum N_i^2\ var\ p_i$$

$$= \frac{1}{N^2} \sum N_i^2 \frac{\sigma_i^2}{n_i} = \sigma_A^2$$

In general, for a given amount of sampling effort, the total number sampled ($= n$) is constant, but the values n_i can vary.

Thus the best design of type A is that in which σ_A^2 is a minimum, subject to $\sum n_i = n$, and this is achieved if $n_i^2 \propto N_i^2 \sigma_i^2$

$$\text{i.e. } n_i \propto N_i \sigma_i$$

If the members of the sample are independent, and form only a small part of the population, then the sampling is approximately binomial

$$\therefore \sigma_i^2 = \pi_i (1 - \pi_i) \quad \ldots\ldots(1.16)$$

$$\text{and} \quad \sigma_B^2 = \frac{1}{n} \pi (1 - \pi) \quad \ldots\ldots(1.17)$$

For σ_A to be a minimum $n_i = c N_i \sqrt{\pi_i (1 - \pi_i)}$ where c = constant.

$$\therefore c \sum N_i \sqrt{\pi_i (1 - \pi_i)} = \sum n_i = n \quad \ldots\ldots(1.18)$$

$\therefore$ the minimum value of σ_A^2 is

$$min\ \sigma_A^2 = \frac{1}{N^2} \sum N_i^2 \frac{\pi_i (1 - \pi_i)}{c N_i \sqrt{\pi_i (1 - \pi_i)}}$$

$$= \frac{1}{cN^2} \sum N_i \sqrt{\pi_i (1 - \pi_i)}$$

$$= \frac{1}{N^2} \cdot \frac{1}{n} \left\{ \sum N_i \sqrt{\pi_i (1 - \pi_i)} \right\}^2 \quad \ldots\ldots(1.19)$$

From (1.17) and (1.19) the variances for the two designs may be compared.

Let $N_i \pi_i = x_i^2$

$$N_i (1 - \pi_i) = y_i^2$$

$$\therefore N\pi = \sum x_i^2 \quad N(1 - \pi) = \sum y_i^2$$

$$\therefore nN^2_{min}\ \sigma_A^2 = (\sum x_i y_i)^2$$

$$nN^2 \sigma_B^2 = \sum x_i^2 \sum y_i^2$$

$$\therefore nN^2 \left\{ \sigma_B^2 - {}_{min}\ \sigma_A^2 \right\} = \sum_{i=1}^{k} x_i^2 \sum_{j=1}^{k} y_j^2 - \left(\sum_{1=i}^{k} x_i y_j \right)^2$$

where k = no. of strata

$$= \sum_{i,j=1}^{k} \left(x_i y_j - x_j y_i \right)^2 \quad \ldots\ldots(1.20)$$

Now the right hand side of (1.20) is a sum of squares, and hence must be positive or zero, and only zero if all of its terms are zero, i.e., if

$$x_i y_j - x_j y_i = 0 \text{ for all } i, j$$

$$\therefore x_i^2 y_j^2 = x_j^2 y_i^2$$

$$\therefore N_i \pi_i N_j (1 - \pi_j) = N_j \pi_j N_i (1 - \pi_i)$$

$$\therefore \pi_i = \pi_j$$

$\therefore n N^2 \left\{ \sigma_B^2 - {}_{min}\ \sigma_A^2 \right\} = 0$ if and only if all the π_i's are equal, and otherwise is positive.

Thus, if the values of n_i are chosen correctly, i.e. proportional to $N_i \sigma_i$, then the variance under design A cannot be greater than that under design B and will generally be smaller ; the greater the dissimilarity between strata the greater is the advantage of A. The proper value of n_i is determined by N_i and $\pi_i (1 - \pi_i)$ neither of which may be known ; however, $\pi_i (1 - \pi_i)$ varies only slowly with variations of π_i over moderate values—as π_i varies from 0·2 to 0·5, $\pi_i (1 - \pi_i)$ varies from 0·16 to 0·25 and so even a rough estimate of π_i will give quite an accurate value for $\pi_i (1 - \pi_i)$. Even when these are known, practical difficulties may prevent n_i taking the desired values. Each week at Lowestoft only a dozen fish of any particular length-group are taken for age determination ; it would be impossible to allocate these few precisely if it were desired to treat each day's landings as a separate strata. In contrast, if all the strata are similar, and all

π_i's the same, then the variance with unstratified sampling will be equal to the smallest obtainable with stratified sampling and, of course, will be less than that obtained with a poor design of stratification. Both designs will give unbiased results so long as the sampling is properly random, but it is easier to take truly representative samples from a short period, or a small number of landings than from a long period, or large number. It is likely that some strata are easier to sample from than others and so may be over-represented in the total sample ; this will give rise to bias under the unstratified design which will not happen for a stratified design. For instance, many fisheries are markedly seasonal and during the periods with lighter landings, it is possible to sample a bigger proportion of the landings and hence these periods will be over-represented in the samples.

Stratified sampling will be advantageous when the total population can be split up into separate strata which are not too similar and when the size of the sample from each stratum can be properly chosen. The finer the sub-divisions, the more similar will be the strata and the more difficult the choosing of the sample size, and there is a limit beyond which sub-division will not be advantageous. This limit will depend on the total sample size and the heterogeneity of the population ; with bigger total samples or greater variation in the population it is more profitable to make finer sub-divisions. At Lowestoft the size composition of the autumn herring shoals varies comparatively rapidly and the measurements are dealt with by weeks (Hodgson 1939) ; the composition of the plaice landings remains relatively steady and are worked up in months. The exact choice of the design of sub-division is not very critical ; the variance of the final estimate will not change much with a change in design when the difference between possible strata is about the same as the difference between the actual allocation of n's and the ideal allocation. The final choice of design will be decided by the comparative ease of sampling and working up the different designs. Where there is a marked difference between strata the advantage of using stratified sampling can be extremely large, often reducing the variance by several times.

The problem of stratification also arises in a slightly different form after the sampling work is done ; then there is still a choice of procedure in analysing the data, but no longer a choice of the n's. However, for large random samples $n_i \propto N_i$ and this is not very different from the theoretical best arrangement of $n_i \propto N_i \sigma_i$. Again, a stratified procedure will be profitable for a fairly heterogeneous population. However, with very small samples and only a few in each stratum the errors of random sampling will cause the n_i to depart by an appreciable percentage from their ideal value. That is, some strata will have too few samples in them, and hence the estimates from them will have an over-large variation, which is not compensated by extra accuracy in other strata.

In length measurements, the most important stratification is the sorting of fish into market categories based on size. When this is done it is virtually impossible to take a single random sample from a landing and a sample has to be taken from each category. From here two procedures are possible : (i) to find the length distribution of each sampled ship and add these together to get that for all sampled ships, finally, by multiplication by the appropriate factor to get the total landings ; or (ii) to follow this procedure for each category individually, getting the length distribution within the total landings of each category and adding to get the grand total. A hypothetical example will make the difference clear. Suppose there are only two categories, large and small, and we take a sample from a ship which has landed 100 cwt. of large and 200 of small out of a total of 1,000 cwt. large and 5,000 cwt. small. Suppose also that of a certain length-group there are 20 fish per cwt. in the large category, and only 2 per cwt. in the small. By procedure (i) in the sampled ship there are, of the required size, $20 \times 100 = 2{,}000$ fish in the large and $2 \times 200 = 400$ fish in the small $= 2{,}400$ fish, and this ship contains 300 out of the total landings of 6,000 cwt. $= \frac{1}{20}$.

$\therefore$ Total number of fish of required length-group landed $= 20 \times 2{,}400 = 48{,}000$.

But by procedure (ii), the sampled ship landed $\frac{100}{1000} = \frac{1}{10}$ of all large, and $\frac{200}{5000} = \frac{1}{25}$ of small

$\therefore$ Number of fish in the large $= 10 \times 2{,}000 = 20{,}000$

Number of fish in the small $= 25 \times 400 = 10{,}000$

$\therefore$ Total number of fish of required length-group landed $= 30{,}000$.

This big difference is because the sampled ship contained a much greater fraction of large fish than did the landings as a whole ($\frac{1}{3}$ as against $\frac{1}{6}$) and the particular size considered is contained chiefly among the large. This difference is not a bias—some other ship contains less than the normal proportion of large and this other ship is (or should be) equally likely to be sampled. It would be a source of bias if samples tended to come consistently from ships with a big proportion of large. In any case, there is a big variation by the first method—the estimate would have been the same if the remaining ships had landed 4,800 cwt. of large + 900 cwt. of small, instead of vice versa—and the true number landed is probably nearer 30,000 than 48,000.

The landings, supposedly sorted throughout the year, will normally be divided into separate periods and as suggested by the general theory, these periods should be of such a duration that there is comparatively little variation in length distribution within the period and that the size of sample is near to the theoretical value. There is no theoretical reason why the periods used should all be of the same duration, though in practice uniform periods are more convenient.

Other possible stratifications of the landings are by type of ship, type of gear, and place of capture. Of these, only a very broad division by areas is likely to provide the necessary differences of length distribution between strata and, from the point of view of estimating the landings, stratification on these lines is not important. However, when attempting to estimate the actual population (in the biological sense) of fish in the sea from a knowledge of the landings, sub-division by place of capture becomes of much greater importance, and this will be discussed in Part II.

The methods of stratification that might be applied to an analysis of the English trawl catches of North Sea plaice are examined in the following tables and diagrams. In Table 1.6 is shown a

TABLE 1.6

Estimates and variances of numbers of different length-groups of plaice landed by Lowestoft trawlers October-December 1950, using three methods of estimation

Length Group (cm.)	20–24	25–29	30–34	35–39	40–44	45–49	50–54	55 +
				Variances x 10^{-6}				
Method (i)	42·58	18,249	2,778	392·7	132·5	29·42	16·48	8·78
Method (ii) (Categ.)	29·56	2,174	1,320	143·5	30·8	14·73	3·50	2·99
By Areas	32·68	14,224	3,301	626·5	147·3	35·06	10·38	6·56
				Estimated Numbers Landed				
Method (i)	26,811	2,063,094	932,486	276,487	132,618	66,012	35,502	22,224
Method (ii) (Categ.)	28,556	2,212,544	952,005	267,168	118,557	58,978	31,833	19,456
By Areas	22,622	2,036,890	974,916	295,456	128,845	66,620	32,765	18,397
i)—(ii)	−1,745	−149,450	−19,519	+9,319	+14,061	−7,034	+3,669	+2,768
St. Dev. of (ii) ...	5,437	46,621	36,330	11,979	5,553	3,838	1,871	1,728

detailed analysis of the Lowestoft landings in October-December 1950. This gives, for each 5 cm. length-group, the estimated numbers landed and their variances, firstly with no account taken of categories (procedure (i) above), secondly using the categories (procedure (ii)), and thirdly by dividing the landings into areas. In this last, the North Sea was divided into 5 areas and the landings from each area estimated separately, using procedure (i) ; these being added to give the total landings. Of the three variances, the second is by far the smallest, the other two differing little. A minor but interesting result is that the difference between the estimates by methods (i) and (ii) is for the 25–29 and 40–44 cm. length-groups, over twice the standard deviation of

method (ii). This implies that the estimate obtained by method (i) is outside the probable range of the true value ; as this is the method often used and in fact originally used on these data, the fact that the estimates obtained by it can be shown to be inaccurate without any extra sampling (by using an improved method of analysis) is rather striking.

The table also shows that although some improvement is made by treating landings from different areas separately, it is not large, and probably not worth the extra calculations involved. This is true despite the fact that there are very noticeable differences in size between areas. If account is taken of categories, then the difference between areas that affects the accuracy of the result will not be the differences in overall length distributions but only the differences in lengths of fish of the same category landed from different areas. These latter differences are likely to be very small, if they exist at all, and hence little advantage is to be expected from treating areas separately, as far as knowledge of the landings are concerned.

Table 1.7 gives the percentage length compositions of fish caught by Lowestoft motor and steam trawlers in the biological year 1950-51. There is very little difference, and presumably even less difference between length distributions of one category. Table 1.8 gives the percentage of

TABLE 1.7

Percentage length composition of landings of plaice by Lowestoft steam and motor trawlers, April, 1950-March, 1951

Length Group (cm.)	20–24	25–29	30–34	35–39	40–44	45–49	50–54	55–59	60–64	65+
Steam Trawlers	0·4	46·4	31·8	12·2	5·4	2·2	1·1	0·4	0·09	0·01
Motor Trawlers	0·7	46·1	33·3	11·7	4·8	2·2	0·9	0·3	0·04	0·01

TABLE 1.8

Percentage length composition, by months, of Lowestoft plaice landings, April, 1950-March, 1951

Month \ Length Group (cm.)	20–24	25–29	30–34	35–39	40–44	45–49	50–54	55–59	60–64	65+
April	0·4	68·2	21·6	6·6	2·1	0·7	0·3	0·1	0·04	—
May	0·3	36·1	34·1	17·6	7·3	2·9	1·2	0·4	0·12	0·01
June	0·3	40·4	41·2	12·0	3·7	1·6	0·6	0·2	0·01	0·00
July	0·2	36·7	40·8	14·1	4·7	2·3	0·9	0·3	0·02	0·01
August	—	44·7	40·3	9·1	3·2	2·0	0·6	0·1	0·01	—
September	0·7	55·7	34·4	5·9	1·8	1·1	0·3	0·1	0·01	0·00
October...	0·8	63·6	26·7	5·6	2·0	0·9	0·3	0·1	0·01	0·00
November	0·5	59·3	29·3	6·5	2·3	1·2	0·6	0·3	0·04	—
December	1·1	41·1	20·5	15·5	10·6	5·5	3·2	2·1	0·26	0·12
January	0·4	31·5	36·3	17·6	7·7	3·7	1·9	0·7	0·18	0·01
February	0·6	30·6	35·4	19·1	8·9	3·3	1·5	0·5	0·13	0·02
March	1·4	54·4	24·2	11·3	6·3	1·7	0·6	0·1	0·03	0·00
YEAR	0·5	46·3	32·5	12·0	5·1	2·2	1·0	0·3	0·07	0·01

each of the chief length-groups in the landings at Lowestoft during each month of the 1950-51 brood-year ; these vary widely. Reducing the period to, say, a fortnight, decreases the difference between periods and makes it less likely that the same proportion of the landings are measured

n each period. This, together with the extra clerical work involved make it unprofitable to treat each fortnight separately. Also, when the fishing vessels are away for periods varying from a few days up to a fortnight, landings only a few days apart will contain fish caught at the same time and too fine a sub-division of landing times becomes unreal.

FIG. 1.2. Length composition of plaice landings at Grimsby and Lowestoft; percentage, by numbers, in each 5 cm. length group, to show differences between the ports, Grimsby having relatively more large fish.

Finally, the landings can be divided according to the port. Fig. 1.2 gives the length composition of the landings at Lowestoft and Grimsby. There is a marked difference between the ports; at Grimsby considerably more large fish are landed.

These facts are sufficient to determine fairly definitely the method of analysing the length distribution of the catches of plaice by English North Sea trawlers. Firstly, the data from Lowestoft and Grimsby are kept separate throughout, though Lowestoft motor and steam trawlers are not separated. At each port the landings during one month form a separate stratum, which are later combined to give the landings for the whole year. At Lowestoft, where the sorting is done by the 'lumpers' on the market, due account is taken of the market categories. At Grimsby, such sorting as does take place is done at sea, and as a result is very variable, consisting of one, two or (most commonly) three main categories instead of the relatively well-defined Large, Medium and Small at Lowestoft. No account is therefore taken of categories. Finally, at both ports no distinction is made of the area of capture for the purposes of obtaining the monthly length composition, so long as it is within the North Sea.

This illustrates the type of considerations needed in deciding a good method of analysing market measurement data, though the answers obtained may differ greatly in different fisheries.

Age determination

The age of a fish cannot always be determined exactly when reading an otolith or scale, e.g. a fish six years old may sometimes be recorded as five or seven years old, and when this difference is due to some variation in the structure of the otolith or scale, rather than in a simple error of observation, it is extremely difficult to detect. Lacking any absolute measurement of true age, a comparison can be made between the 'otolith' ages as read by different observers, or between the 'otolith' and 'scale' ages. Any differences that appear will give an idea of part of the difference between the 'otolith' age and the true age, though it may be a very severe under-estimate of the total difference. However, it is possible to calculate what the effect will be of various errors in the age determinations.

Let us suppose at first that the error in reading the age is only one year up or down, and that for a fish actually n years old—

a_n = probability of being considered as $n - 1$ years old

$1 - a_n - b_n$ = " " " " " n years old

b_n = " " " " " $n + 1$ years old

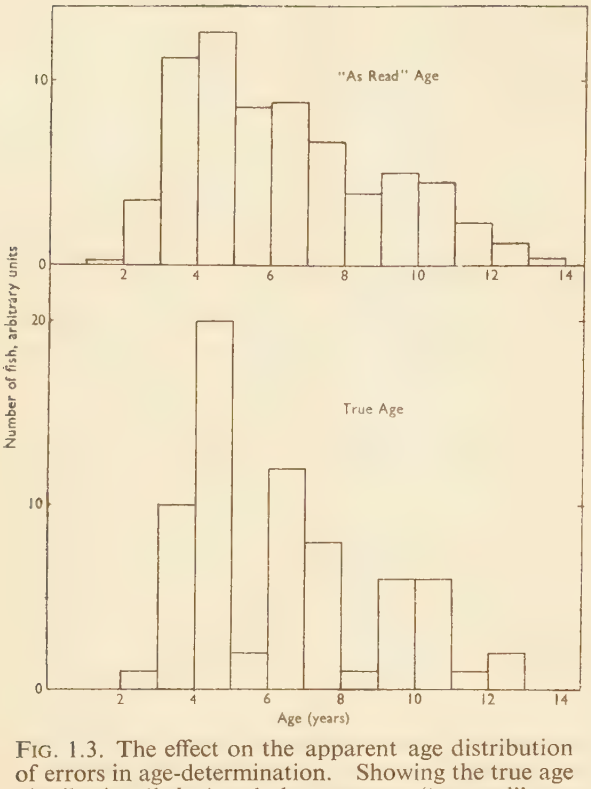

FIG. 1.3. The effect on the apparent age distribution of errors in age-determination. Showing the true age distribution (*below*) and the apparent "as read" age distribution (*above*) when 50% of the age determinations are wrong.

For a perfect age determination $a_n = 0$ $= b_n$. It is likely that the a and b's are not the same for all n, in general increasing with increasing age ; i.e., older fish are more difficult to age correctly.

Suppose the true numbers of fish of age n are N_n, then of these $(1 - a_n - b_n)\ N_n$ are considered to be of age n and $a_n N_n$ and $b_n N_n$ of age $n - 1$ and $n + 1$ respectively. Then M_n, the estimated numbers of age n is given by $M_n = b_{n-1} N_{n-1} + (1 - a_n - b_n) N_n + a_{n+1} N_{n+1}$ and thus will contain contributions from three year-classes. The general effect is to reduce the apparent differences between year-classes, levelling out the age distribution, though keeping the same general shape. This is shown in Fig. 1.3 for $a_n = 0{\cdot}3$, $b_n = 0{\cdot}2$ for all n ; i.e., a case where only 50 per cent of the ages are read correctly ; the bottom figure shows the true age and the top the apparent age distribution. Though the differences have been markedly reduced, the year-classes aged 4, 6, 9 and 10 are still apparent as good ones and 5 and 8 are poor ones. More important is that the apparent average age is unaltered and that the rate at which the strength of year-classes declines from a maximum at 3–4 years until a virtual extinction at 13–14 years, remains essentially the same. As estimates of mortality rates are of prime importance in any population study, the effect of inaccurate age determination on them are worth more detailed examination.

If N_n, M_n are the real and apparent densities of a year-class in one year, and N'_{n+1} M'_n those of the same year-class in the next year, we have in our notation :

$$M_n = b_{n-1} N_{n-1} + (1 - a_n - b_n) N_n + a_{n+1} N_{n+1} \quad \text{.....(1.21)}$$

$$M'_{n+1} = b_n N'_n + (1 - a_{n+1} - b_{n+1}) N'_{n+1} + a_{n+2} N'_{n+2} \quad \text{.....(1.22)}$$

assuming the errors in age determination are the same from year to year.

Now let λ and μ be the true and apparent survival rates and suppose these are the same for all ages : then

$$N'_{n+1} = \lambda N_n \text{ and } M'_{n+1} = \mu M_n$$

and equation (1.22) becomes

$$\mu M_n = b_n \lambda N_{n-1} + (1 - a_{n+1} - b_{n+1}) \lambda N_n + a_{n+2} \lambda N_{n+1} \quad \text{.....(1.23)}$$

$\therefore$ from equations (1.21) and (1.23)

$$\mu = \lambda \frac{b_n N_{n-1} + (1 - a_{n+1} - b_{n+1}) N_n + a_{n+2} N_{n+1}}{b_{n-1} N_{n-1} + (1 - a_n - b_n) N_n + a_{n+1} N_{n+1}} \quad \text{.....(1.24)}$$

If all the b's and all the a's are the same, i.e. the errors in age determination are the same for all ages, then (1.24) reduces to $\lambda = \mu$ and the survival rates are unaffected by the errors. Normally, though, age determination becomes increasingly uncertain with older fish and the errors are not constant. If the size of the year-classes are not too different, or averages are taken over a period, then N_n, N_{n+1}, etc. will be related by—

$$N_{n+1} = \lambda N_n = \lambda^2 N_{n-1} \quad \ldots\ldots(1.25)$$

$\therefore$ equation (1.24) becomes

$$\mu = \lambda \frac{b_n + (1 - a_{n+1} - b_{n+1})\lambda + a_{n+2}\lambda^2}{b_{n-1} + (1 - a_n - b_n)\lambda + a_{n+1}\lambda^2} \quad \ldots\ldots(1.26)$$

$$\therefore \mu = \lambda \frac{A}{B}$$

where $A - B = \{b_n + (1 - a_{n+1} - b_{n+1})\lambda + a_{n+2}\lambda^2\}$
$$- \{b_{n-1} + (1 - a_n - b_n)\lambda + a_{n+1}\lambda^2\}$$
$$= b_n - b_{n-1} - \{(a_{n+1} - a_n) + (b_{n+1} - b_n)\}\lambda + (a_{n+2} - a_{n+1})\lambda^2 \quad \ldots(1.27)$$

λ is less than 1 and often quite small, so that the first term in this expression will usually be the largest, and as the error tends to increase with age, $b_n > b_{n-1}$. Hence the right hand side is positive and $A - B > 0$; $A > B$. The errors, therefore will make $\mu > \lambda$ i.e. over-estimate the survival rate. The extent of this can be illustrated by examples.

Let $\lambda = 0{\cdot}5 \quad b_{n-1} = 0{\cdot}1 \quad b_n = 0{\cdot}2 \quad b_{n+1} = 0{\cdot}3 \quad a_n = a_{n+1} = a_{n+2} = 0$

$$\text{then } \mu = \lambda \times \frac{0{\cdot}2 + (1 - 0{\cdot}3)\,0{\cdot}5}{0{\cdot}1 + (1 - 0{\cdot}2)\,0{\cdot}5} = \lambda \frac{0{\cdot}2 + 0{\cdot}35}{0{\cdot}1 + 0{\cdot}40}$$

$$\therefore \mu = 1{\cdot}1\,\lambda$$

or suppose $\lambda = 0{\cdot}25 \quad b_{n-1} = 0 \quad b_n = 0{\cdot}2 \quad b_{n+1} = 0{\cdot}4 \quad a_n = a_{n+1} = a_{n+2} = 0$

$$\text{then } \mu = \lambda \times \frac{0{\cdot}2 + (1 - 0{\cdot}4)\,0{\cdot}25}{0 + (1 - 0{\cdot}2)\,0{\cdot}25} = \lambda \frac{0{\cdot}2 + 0{\cdot}15}{0{\cdot}2}$$

$$\therefore \mu = 1{\cdot}75\,\lambda$$

finally, let $\lambda = 0{\cdot}5 \quad b_{n-1} = 0{\cdot}3 \quad b_n = 0{\cdot}32 \quad b_{n+1} = 0{\cdot}34$
$a_n = 0{\cdot}2 \quad a_{n+1} = 0{\cdot}22 \quad a_{n+2} = 0{\cdot}24$

$$\text{then } \mu = \lambda \frac{0{\cdot}32 + (1 - 0{\cdot}22 - 0{\cdot}34)\,0{\cdot}5 + 0{\cdot}24\,.\,0{\cdot}25}{0{\cdot}30 + (1 - 0{\cdot}20 - 0{\cdot}32)\,0{\cdot}5 + 0{\cdot}22\,.\,0{\cdot}25} = \lambda \frac{0{\cdot}600}{0{\cdot}595}$$

$$\therefore \mu = 1{\cdot}0084\,\lambda$$

Thus in these examples the survival rates are over-estimated by 10 per cent, 75 per cent and 0·84 per cent respectively ; in the second example 40 per cent of the $(n + 1)$ age-group are read incorrectly, while all the $(n - 1)$ age-group are correct, and this is an extreme change of error. The first is probably as bad as will occur in practice, giving a 10 per cent error, which does not make the estimate of survival useless. The third example shows how little the survival rates are affected by even 50 per cent incorrect age determinations, provided the errors do not change fast. These calculations, made for an error of only one year, easily extend to two or more years, with similar results. The growth curve will suffer some distortion because the fish apparently of, say, seven years old will contain some of other ages and the average age will not be seven years. Thus when the growth curve of size against age is plotted, the points will be to one side of their correct position, but again, so long as this error is reasonably consistent the whole curve is moved bodily and the shape preserved with little distortion. In the type of error considered so far the shift will probably be only a fraction of a year.

Errors of age determination become extremely serious when the estimated age ceases to be, even on the average, the same or nearly the same as the true age ; e.g., fish truly, say, five years old are estimated as say 8, 9 and 10, rather than 4, 5 or 6 years. No useful estimate of growth, mortality or strength of year-classes can then be made. A good idea of the accuracy of age composition comes from a study of the changes of the age composition from year to year. If a strong or poor year-class can be followed through from recruitment until nearly all its members are dead, then the age determinations must be substantially correct, and estimates of growth and mortality made with confidence, though the difference between year-classes may be under-estimated. The different methods of age determination, and of checking one with another are discussed in greater detail by Graham (1929).

Often there are fish whose age cannot be stated with certainty, but can be aged to within a year or so, e.g., being recorded as 6 ?. The proportion of these tends to increase with increasing age, and for the plaice a large part of the oldest fish are recorded as doubtful and these cannot be omitted from the calculations without a serious bias towards under-estimating the abundance of older fish.

The numbers of fish of each age landed can be determined in exactly the same way as the numbers in different length-groups and the theory of the preceding sections applied directly. While several hundred length measurements can be made in an hour, age determination is a much longer process and it is very desirable to cut down the number of fish which are aged. This can be done by using length distribution as an intermediate step and is particularly advantageous for fish that are growing quickly and uniformly. This method has been used for several fish, e.g., herring (Hodgson, (1939)) and cod (Fridriksson, (1934), Graham, (1938)) and is the standard practice for the English plaice investigations. Samples are taken from each length-group and the ages of each fish, and the age distribution within each length-group determined. The total landings of each length-group are then split up by ages in the same proportions as in the corresponding length-group in the sample. The total number of each age can then be found by adding the contributions from each length. Thus, if N_i fish of the i^{th} length-group are landed, and a total of n_i of them are examined for age, among which $n_i\, p_i$ are of a certain age, then we can write—

$$
\begin{aligned}
p_i &= \text{proportion of given age in } i^{th} \text{ length-group} \\
var\ p_i &= \frac{1}{n_i}\, p_i\,(1 - p_i), \text{ by the binomial distribution} \\
N_i\, p_i &= \text{number of given age landed in length-group} \\
\therefore\ var\ N_i\, p_i &= N_i^2\ var\ p_i + p_i^2\ var\ N_i \qquad \text{.....(1.28)} \\
&\qquad \text{(as } N_i \text{ and } p_i \text{ are independent)}
\end{aligned}
$$

The second term in 1.28 is because N_i will not normally be known exactly but is only an estimate obtained from the length measurements. The variance of the total number landed of any age, regardless of size, is determined by summing the variances within each size, and if N_p is the estimated total number landed—

$$
\begin{aligned}
N_p &= \sum N_i\, p_i \\
var\ N_p &= \sum N_i^2\ var\ p_i + \sum p_i^2\ var\ N_i
\end{aligned}
$$

The method of calculation is best demonstrated by a worked example. In Table 1.9 the calculations to give the age distribution of the Lowestoft plaice landings for 1952-3 are shown. For each 5 cm. length-group are shown, in the first two columns, the total numbers landed, as estimated from measurements on the market, and the number of fish examined for age. The number $n_i\, p_i$ and proportion p_i at each age of the latter are shown as the upper two figures in the succeeding columns ; the lowest figure is the estimated number $N_i\, p_i$ of fish landed of that size and age. For each age this last is summed for all sizes to give the figure at the foot of the column, the estimated total number of that age landed.

Ketchen (1950) has used an age-length key, with stratified sub-sampling, to determine the age distribution of samples of Pacific flounders. Though his use of χ^2 is not strictly valid, he showed that taking 10 or 15 fish at each length gave estimates which differed little from the whole sample, though sub-samples of only 5 showed some divergence. Usually exact knowledge of the composition of each sample is less important than a general knowledge of the whole population, and the labour saved in taking sub-samples of only 5 could probably be used in taking sufficient extra samples to more than compensate for the loss in accuracy in individual samples. An extreme example of such sampling has been given for the halibut by McIntyre (1953) who showed that certain length-groups of small fish could be distinguished as containing fish of only one age, and hence for these groups only one age determination is necessary.

This scheme has the usual advantages of a stratified sampling design. It eliminates any bias caused by the age samples containing too many or too few large fish and by a suitable choice of the size of sample within each length-group the accuracy may be improved. The latter advantage may be small because of the conflicting requirements of fish of different ages. To estimate the numbers of young fish with greatest accuracy, sampling must be concentrated on the small fish and vice-versa for the older fish. When the age samples are taken regardless of length, there will of course be a preponderance of small fish and when the variances are calculated, usually

TABLE 1.9

Age-Length key and calculations, for Lowestoft plaice landings, April, 1952-March, 1953

Length Group	Number Landed (N)	Number Examined (n)		Age										
				II	III	IV	V	VI	VII	VIII	IX	X	XI	XII+
25–29 cm.	9,708,577	360	np	16	99	101	125	18		1				
			p	0·0444	0·2750	0·2806	0·3472	0·0500		0·0028				
			Np	431,061	2,669,858	2,724,227	3,370,818	485,429		27,184				
30–34 cm.	9,258,540	359	np		13	57	172	87	27	1	2			
			p		0·0362	0·1588	0·4791	0·2423	0·0752	0·0028	0·0056			
			Np		335,159	1,470,256	4,435,767	2,243,344	696,242	25,924	51,848			
35–39 cm.	2,835,767	359	np		1	15	84	136	77	19	15	9	1	2
			p		0·0028	0·0418	0·2340	0·3788	0·2145	0·0529	0·0418	0·0250	0·0028	0·0056
			Np		7,940	118,535	663,570	1,074,189	608,272	150,012	118,535	70,894	7,940	15,880
40–44 cm.	920,773	240	np			3	25	54	66	28	24	17	12	11
			p			0·0125	0·1042	0·2250	0·2750	0·1167	0·1000	0·0708	0·0500	0·0458
			Np			11,510	95,944	207,174	253,213	107,454	92,077	65,191	46,039	42,171
45–49 cm.	390,249	238	np			1	7	24	37	34	24	15	23	73
			p			0·0042	0·0294	0·1008	0·1555	0·1429	0·1008	0·0630	0·0967	0·3067
			Np			1,639	11,473	39,337	60,684	55,767	39,337	24,586	37,737	119,689
50–54 cm.	153,218	237	np				2	5	19	15	14	15	30	137
			p				0.0084	0·0211	0·0802	0·0633	0·0591	0·0633	0·1266	0·5780
			Np				1,287	3,233	12,288	9,699	9,055	9,699	19,397	88,560
Total	23,267,124	1,793		431,061	3,012,957	4,326,167	8,578,859	4,052,706	1,630,699	376,040	310,852	170,370	111,113	266,300

the coefficients of variation will increase sharply with age. While the numbers of young fish are known accurately, those of the old fish are relatively inaccurate, and this is generally undesirable, especially for the calculation of mortality rates. By taking proportionately more large fish for age determination this can be corrected, so that for at least all the commoner ages, the numbers are estimated with equal percentage accuracy.

The age and length data of Lowestoft plaice landings in January and February, 1950, have been analysed to determine the variance under different methods of calculation and the results are shown in Tables 1.10 and 1.11. During the two months four samples were taken, each consisting of a ten stone box from which all the fish were examined and their age determined. The first part of Table 1.10 shows the estimates and variances obtained by using these samples directly without reference to the length distribution. As only four samples were taken, the variances are

TABLE 1.10

Numbers and variances of age-groups of plaice landed at Lowestoft in January and February, 1950, as estimated by different methods

Age	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII+
	Direct Age Sample										
Numbers $\times 10^{-3}$ ...	191	986	1,621	610	290	154	179	148	80	55	123
Variance $\times 10^{-6}$ ...	3,680	98,300	119,000	22,300	3,780	645	4,490	304	1,150	1,660	1,320
Coeff. of Var. ...	31·8	31·8	21·3	24·4	21·2	16·5	37·4	11·8	42·4	74·0	29·5
	Age-length Key										
Numbers $\times 10^{-3}$ ...	215	1,114	1,870	689	321	153	172	127	70	52	88
Variance $\times 10^{-6}$ ...	1,540	8,300	13,100	4,340	2,070	875	932	646	378	299	288
Coeff. of Var. ...	18·3	8·2	6·1	9·6	14·2	19·3	17·7	20·0	27·7	33·3	19·3
	Age-length Key (revised numbers)										
Variance $\times 10^{-6}$ ...	2,990	12,300	17,400	5,400	2,270	671	632	388	232	222	161
Coeff. of Var. ...	25·4	10·0	7·1	10·7	14·9	16·9	14·6	15·5	21·7	28·7	14·4

TABLE 1.11

Detailed analysis to give numbers and variances of plaice age VIII in Lowestoft landings in January and February, 1950, as estimated by age-length key

Length Group (i)	30–34 cm.	35–39 cm.	40–44 cm.	45–49 cm.	50–54 cm.	Total
Number landed (N_i)	1,329,911	790,027	271,579	118,338	67,162	
Variance of $N_i \times 10^{-3}$ ...	5,400,386	1,419,952	437,025	188,681	69,036	
Number Otolithed (n_i) ...	177	119	47	23	21	
No. age VIII ($n_i p_i$)	2	9	11	6	1	
Proportion age VIII (p_i) ...	0·0113	0·0756	0·2340	0·2609	0·0476	
Total No. age VIII ($N_i p_i$) ...	15,028	59,726	63,550	30,874	3,197	172,375
$\frac{N_i^2}{n_i} p_i (1 - p_i) \times 10^{-3}$ ...	111,639	366,538	281,280	117,408	9,738	886,602
p_i^2 *var* $N_i \times 10^{-3}$	690	8,116	23,930	12,843	156	45,735
				Total variance $\times 10^{-3}$ =		932,337

not very accurate ; in particular the estimated variances of the VII and IX groups are too low, and those for the VIII and XI groups probably too high. The second part gives the estimates obtained by using an age-length key, as described, while the last part figures for the variances which would be obtained by using a different sampling pattern. This pattern is obtained, not by taking the age samples randomly from all lengths, but by taking proportionately more larger fish. The numbers in each length-group used in the calculations are shown below, with the numbers in the actual sample for comparison.

Length-group (cm.)	20–24	25–29	30–34	35–39	40–44	45–49	50–54	55–59	60+	Total
Actual Numbers	14	313	177	119	47	23	21	4	2	720
Revised Numbers	14	150	150	150	100	100	50	4	2	720

In Table 1.11 the analysis for the VIII group is given in more detail, showing the contribution to the estimate of number and variance from each length. In each length the greater part of the variance is the term $\frac{N_i^2}{n_i} p_i (1 - p_i)$ rather than the term $p_i^2 \, var \, N_i$, that is sampling errors in the age-length key, rather than in the abundances of each length. Greater accuracy will be obtained by making more age determinations, but not to any extent by improving the accuracy of the length measurements.

Examination of Table 1.10 shows that except for two ages (VII and IX) where it is slightly higher, the variance using an age-length key is lower, and usually very much lower, than using the age samples directly ; for the III group the latter is more than ten times the variance using an age-length key. The coefficient of variation using the key increases very steadily with age, from 6 per cent at four years to 33 per cent at eleven years, but using the revised sampling design this trend is reduced, but not eliminated. It could, of course, be eliminated or even reversed by taking proportionately more larger fish. In the suggested design, using exactly the same number of age determinations, the accuracy for the older fish has been very much increased—the variance decreased by as much as 40 per cent, without greatly affecting the accuracy for the younger fish.

In the estimates of the numbers landed of each age by the two methods, the main differences lie in the greater numbers of old fish estimated by using age alone. This is due to the size of fish in the four age samples being rather greater than the average size for the landings as a whole. It is, of course, this variation in the average size of fish in the samples which makes the biggest contribution to variance of the estimates using the aged samples alone. This also causes the estimates of numbers of adjacent ages to be strongly correlated, for if, say, too many very large fish occur in a sample, then the numbers in all the very old age-groups will be over-estimated. This can easily be seen by comparing the estimates with those obtained by using an age-length key which may be assumed to be comparatively correct. For all the ages from II to VI the latter are considerably bigger, the difference being usually rather more than the standard deviation of the age-length estimates. For the VII and VIII groups the two estimates are virtually the same, while the direct age estimates for the numbers in the older age-groups are all larger than those from an age-length key.

Using the age-length key, where variations in the estimates are caused by variations in the number of the particular age at one length, one age will be over-estimated when it is over-represented within a length-group ; this will tend to make other and particularly adjacent ages, underrepresented, so that adjacent ages will tend to be negatively correlated. For most population work, and especially in estimating mortality rates, it is a definite disadvantage to have a marked positive correlation between the numbers of adjacent ages, and this gives a further reason for preferring the age-length key.

PART II

COMPOSITION OF THE NATURAL POPULATION

Estimation of density of the natural population

Though a knowledge of the composition of the catch is important *per se*, more important is a knowledge of the natural stock from which the catch comes. It is beyond the scope of this paper to attempt any absolute enumeration of the natural stock, but it will attempt to establish a reliable index which will bear a fixed ratio to the density of fish in the area of the fishery.

Though the catch of a known amount of fishing must be related to the total stock of fish, this relationship is complicated by the different capabilities of fishing gears, by the differences in behaviour between various species and sizes of fish, and by the generally uneven distribution of both fish and fishing. These problems have been discussed among others, by Beverton and Holt (in press) from the point of view of determining the mortality caused by a known amount and distribution of fishing, and hence the catch from a given density of fish. The following treatment forms in part the dual of theirs, treating the problem from the point of view of estimating the density, and hence mortality, from known catch and amount of fishing.

Some definitions may be suggested. The *density* of fish is the absolute number or weight of individuals in the population per unit area, but may also be used for what is more properly a *density index*, any number that is proportional, or is presumed to be proportional, to the density, e.g., the catch-per-unit-fishing-effort. The *fishing power* of a vessel, as defined by Beverton and Holt is the ratio between the catch-per-unit-fishing-time of the ship, and that of a standard vessel, when they are fishing at the same time and place, i.e. on the same density of fish. More strictly this may be defined relative to a standard type of fish. Dually, the *vulnerability* of a type of fish may be defined as the ratio of the density of a standard fish to that of the given fish when the catch-per-unit-fishing-time by a standard vessel is the same. The combination of these two factors determines, for a given vessel fishing for a given species, the relation between the catch-per-unit-fishing-time and the density of fish.

In discussing the effects of spatial variation it is possible, in part, to separate the effects of non-random distribution of the fish, and the distribution of the fleet, which is in general a consequence of it. In studying some pelagic fisheries the manner and rate in which the fishing fleet detects and subsequently collects on to the shoals of fish is of prime importance. In this paper, however, only the end result will be considered ; that is, the degree by which the density of fish around the fishing vessel differs from the average density. No distinction will be made between a fishery in which the fish are only slightly unevenly distributed, but the fishing vessels locate very accurately the places of highest density, and a fishery in which the fish are very unevenly spread, but in which the vessels do not follow the shoals so closely. However, a distinction will be made between the effects of uneven distribution within a relatively small area, and within a whole region.

The *aggregation* of the fishing unit or units on the fish is the ratio of the density of fish in the immediate vicinity of the gear to the average density in the general area in which the gear is working. The *concentration* on the fish is the ratio of the average density in this general area, to the average density of the whole accessible stock. Both terms will therefore have a value of unity when the density on which the ships are fishing is the same as the average density, e.g., when the ships are distributed independently of the fish, or when the fish are evenly spread over the whole area. Generally, they will be greater than one, often very much greater for pelagic fish, but may be less for unpopular species, and falling to zero when there is no overlap between the area fished and the area inhabited by the fish. These factors do not necessarily imply anything about the relative positions of the fishing vessels. The aggregation, or concentration, can be high and the ships widely spread, so long as each is on a locally high density of fish. Conversely, the aggregation can be low, but all ships fishing in the same small area, if the density of fish in this area is no greater than the average density. The difference between these factors, and those such as a correlation coefficient, which measures the degree of association between, say, the amount

of fishing and the density of fish, must be emphasized. The definitions suggested may be considered in terms of only one ship, in fact a single trawl haul, or in terms of a whole fleet's activities. The correlation coefficient is only definable in terms of the distribution of a number of ships. Also it cannot take account of the magnitude of the differences in density, but only whether these differences are connected with differences in the amount of fishing. Concentration and aggregation are thus very similar terms, but it is convenient to distinguish between them. The concentration will depend mostly on economic factors, such as variations in the relative prices of different species, and is relatively easy to estimate, given adequate commercial statistics. The aggregation is the interaction between the fish behaviour, particularly shoaling, and the skill of the fishermen, and is difficult or impossible to estimate purely from commercial statistics. The dividing line between the two factors depends on the definition of the general area of fishing, which may be regarded as the area in which the fisherman would say he had been fishing. More exactly, the general area of fishing used later for the North Sea haddock is one or more British statistical rectangles, roughly 30 miles square, though a better area would probably be rather smaller than this.

The combination of all factors may be termed the *availability* which is the factor relating the raw catch of unit fishing effort to the total density. This is similar to the use by Marr (1951), in which availability was defined as the degree to which a population was accessible to a fishery, but different from other American writers who have used it synonymously with catch-per-unit-effort, i.e., as the product of availability and density.

Variations in the availability, which cause the catch-per-unit-effort to be unreliable as a density index have been discussed by Ricker (1940). They include systematic differences between species, or between different sizes or ages in the same species, steady long-term changes, seasonal changes and short-term fluctuations. These last, in so far as they are due to such random effects as weather, may be expected to have little effect when computing the density over a whole year, but may be important for short fishing seasons. The vulnerability is particularly liable to such fluctuations ; for instance many pelagic fisheries are affected by the phases of the moon (Savage and Hodgson (1934), and Clark and Daugherty (1950)), and during north-east winds the catches of demersal fish in the southern North Sea are greatly reduced.

Silliman and Clark (1945) have analysed the effect of the phase of the moon and wind conditions on the Californian sardine catches by a multiple correlation, and thus derived a formula with which to adjust the observed catch. This adjusted catch, divided by the observed effort, gives an estimated catch-per-unit-effort unaffected by weather conditions. This is, of course, in effect, estimating the changes in vulnerability and applying a correction factor to the catch-per-unit-effort, and gives a density index unaffected by these changes. The authors concluded that the differences between the uncorrected figures and the adjusted ones, including a correction for the actual time spent scouting for fish, was small enough to be unimportant, at least to the degree of accuracy required. Over a whole season the effects of the weather nearly average out, but corrections for weather become important in comparing periods for which the average weather might be appreciably different, e.g., single weeks. Some differences in availability are obvious, such as the escape of small fish through the meshes of a trawl, so that any density index obtained can only refer to fish larger than the selection size of the mesh used. Other differences may only become apparent when two types of gear are fished side by side. Then if the composition of the catches, apart from their absolute magnitude, differs significantly, then the vulnerability to at least one of the gears must be non-uniform. When English and Scottish research vessels fished side by side, with trawls used typically to catch plaice and haddock respectively, the English vessel caught more plaice, but far fewer haddock, (Parrish 1951). This may be considered either as a great difference in vulnerability between the two species relative to the two ships, or as a difference in relative fishing power of the two ships as measured by the two species. This has a very important bearing on the interpretation of commercial catches ; a catch of 40 cwt. of plaice per 100 hours fishing in an area fished mainly for plaice indicates a density considerably less than 40 times that of 1 cwt. of plaice caught per 100 hours fishing in an area fished mainly for haddock.

An even more serious effect was shown by the comparison between long-line and purse-seine catches in the Lofoten cod fishery (Rollefsen 1953), and between the plaice catches of the trawlers *Sir Lancelot* and *Platessa* and the seiner *Arabis* (Margetts 1949), where there is a difference, considerable for the cod, between the size of fish caught by the different gears. For at least one

of each of these pairs of gears the vulnerability must therefore be different for different sizes, and hence ages, of fish. This makes any comparison of the density indices for different ages, and hence estimates of the mortality rates, unreliable. Fortunately, at least for the Lofoten fishery, it is reasonable to assume that the differences are caused by only one of the pair—the long-line—and that the purse-seine is by its nature unselective. Density indices undistorted by the selective effect may therefore be obtained by using the purse-seine catches alone.

Some evidence of a third form of systematic variation in the vulnerability has been given by Hickling (1931). When the catches of hake by trawlers using the then new Vigneron-Dahl gear were compared with those of the ordinary otter trawl, they were relatively greatest when the absolute size of catch was greatest. In heavy fishing the V.D. gear apparently outfished the other by up to 100 per cent, but in light fishing the two caught almost equal quantities. If this is real, and not just a chance effect, the vulnerability to at least one of the gears must depend on the stock density. A change in density will either be over-estimated by the V.D. gear, or under-estimated by the normal otter trawl, so that for one gear the catch-per-unit-effort will not be proportional to the true density.

Just as the actual gear is modified for the species of fish particularly required, so the fishing positions are chosen with reference probably to a single preferred species, or even a particular size or condition of fish of one species. Thus the aggregation and the concentration are likely to have considerable systematic differences, so that the aggregation for plaice will be higher in the southern North Sea (a predominantly plaice fishery) than in the northern North Sea (predominantly cod and haddock). As the aggregation depends on the ability of the fishermen to find and catch small local concentrations of fish which may well be more marked at some overall densities of fish than at others, this factor may well not be independent of the density. This may have happened in the plaice of the southern North Sea in 1946. The catch-per-unit-effort, which was 5–6 times the pre-war level in January, declined to only about twice pre-war in November and December. This decline was much more rapid than the amount of fishing is likely to have caused when compared with the mortality caused by the much greater amount of fishing before the war. However, if the aggregation was unusually high in January and decreased during the year, then the rapid decline in catch-per-unit-effort is accounted for in two ways ; firstly, the January figure is an over-estimate, so that part of the decline is artificial, being only a measure of the decrease in aggregation, and secondly, the fishing in the early part of the year would be more effective, and would cause a larger mortality than might be expected purely from the number of hours spent fishing.

Seasonal changes in the availability may include changes in fish behaviour such as spawning movements, if these are reflected in the aggregation or the concentration. Thus the autumn and early winter sees an extremely high concentration on the North Sea herring off the East Anglian coast and later towards the Straits of Dover. The cod in the Barents Sea support large spring and autumn fisheries round Bear Island, where the immature fish congregate in vast shoals, giving a high concentration, but in the summer they are probably much more spread out giving a lower concentration and hence poorer catches.

The long-term changes in availability are probably the most important in studying the fortunes of a fishery. Changes in the behaviour of the fish, e.g., the movements of the herring, have often been important but more general have been changes in the fishing gear and methods of using it. Improvements range from changes in fishing power, relative to an hour's fishing, by the introduction of larger and more powerful vessels, or the introduction of the Vigneron-Dahl gear, to the use of the echo-sounder to give easier location of fish shoals, thus improving the aggregation, or the use of wireless between ships, which can improve the concentration.

On top of these regular changes, any single trawl haul or other unit of fishing effort, will give very variable results, even in apparently identical conditions. In analysing the results of comparative fishing experiments in the North Sea by the research trawlers *Sir Lancelot* and *Explorer*, Parrish (1951) obtained a residual variance of 0·042 in catches of plaice transformed by logarithms. This is equivalent to an average variation of 60 per cent in catches. Similarly Barnes and Bagenal (1951) obtained coefficients of variation between 40 per cent and 85 per cent in catches of half-hour trawl hauls on inshore grounds. Though this may seem a large variation, a coefficient of variation

of 50 per cent in one haul is reduced to one of 0·5 per cent when taking the mean of ten thousand hauls—a not very great amount in a commercial fishery.

In determining the reliability of density index from known catches of fish, whether by commercial vessels or by research vessels, all these possible sources of inaccuracy must be taken into account, though it is only the changes in the various factors and not their absolute magnitudes which are important. For instance, in commercial fishing the aggregation is difficult to estimate and is probably considerably larger than unity, but so long as it does not change, this difference does not affect the validity of the catch per unit effort of the commercial fleet as a density index. The following sections will deal with methods of correcting some of the more accessible of these sources of variability and thus producing more reliable density indices.

The use of a special research ship for sampling purposes can remove some of these sources of variability, but basically an individual trawl haul by a research vessel can give no better information on the fish present on the ground than one by a commercial vessel. The use of a research vessel has its advantages ; its fishing position may be accurately known, the exact specifications of the gear may be known, there is no rejection of fish below the marketable size, and it can use a small mesh to sample fish below the selection size of the commercial mesh. However, fish just below the selection size of the normal mesh can be sampled by authorizing certain commercial trawlers to use an abnormally small mesh, as has been recommended for the Georges Bank haddock (Graham, 1952). Because research vessel data has to be based on only a very small number of hauls, the random errors of some 50 per cent per haul are liable to be very important.

Some of these differences between research vessel and commercial samples are brought out in comparing the two sets of Scottish data on haddock from the Faroes. In Table 2.1 are given the mean of the monthly catch in numbers per 10 hours fishing of each year class of haddock in 1950 and 1951, as caught firstly by the research vessels *Explorer* and *Scotia* and secondly by the Aberdeen commercial trawlers, (data from Jones, 1951, and Jones and Main, 1952). The research vessel data for 1950 have been assumed to be per 1 hour fishing, as appears likely from internal evidence, rather than per 10 hours fishing, as stated.

TABLE 2.1

Catch in numbers of haddock at Faroes per 10 hours trawling by research and commercial vessels

Year Class	1950		1951	
	Research	Commercial	Research	Commercial
1951	—	—	538	—
1950	38	—	360	34·9
1949	602	143·6	253	443·3
1948	616	778·6	71	361·3
1947	65	172·7	6	67·6
1946	6	51·1	2	14·4
1945	15	85·9	4	29·6
1944	19	102·1	7	49·3
1943	—	42·5	—	17·9
1942	—	8·3	—	4·8
1941	—	4·8	—	2·4
1940	—	3·6	—	0·6
1939+	—	1·5	—	1·0

In comparing the two sets of figures, it is obvious, as expected, that the commercial ships do not sample at all properly the youngest fish, i.e. the 1949 and probably the 1948 year-class in 1950 and the 1950 and 1949 year-classes in 1951, though they are sampled by the research vessels. Against this the commercial samples contain members of at least 5 year-classes (1939 to 1943) which are not represented in the research vessel samples. The differences in the variances of the two density estimates are most easily seen from Table 2.2, which gives the percentage survival, i.e. the ratio of the catch per 10 hours fishing in 1950 and 1951, of each year-class, by the two methods. The research vessel sampling provides figures for 7 year-classes, two of which are not fully represented in the samples ; the estimated survival for the 5 other year-classes is highly variable. The commercial samples provide satisfactory estimates for 8 year-classes ; these are all reasonably consistent. The 1949 year-class is of course not fully recruited in 1950 and the 1940 and older year-classes are scarce and therefore liable to great sampling variation, and these year-classes therefore do not give satisfactory survival estimates.

TABLE 2.2

Percentage survival from 1950 to 1951 of Faroe haddock as measured by research and commercial vessels

Year Class	1950	1949	1948	1947	1946	1945	1944	1943	1942	1941	1940	1939+
Research Vessel	947	42	12	9	33	27	37	—	—	—	—	—
Commercial Fleet	—	309	46	39	28	34	48	42	58	50	17	67

Any systematic difference between the commercial and research vessel density indices will appear in the ratios of the catches per 10 hours fishing, and these are given in Table 2.3. The fact that the commercial figure is consistently some six times bigger than that of the research vessel is not in itself of great importance and does not invalidate either figure as a useful density index. It does serve as a measure, partly of the relative catching powers of the different ships, and partly of the aggregation and concentration of the commercial fleet. The important question is whether these ratios have any systematic changes, either from year to year, or from age to age ; the small number makes any definite answer difficult, apart from the obvious differences in the very young fish. If there are no other such systematic differences, then the research vessel has no advantages in sampling the fully exploited stock. If there are systematic differences, then, assuming the research vessel figure to be correct, the commercial fishing effort must be generating an uneven fishing mortality, and therefore it is most important for any proper study of the effect of fishing, that the actual composition of the catches is known. That is, sampling of the commercial catches is always useful ; the use of a research vessel for sampling purposes may sometimes also be important.

TABLE 2.3

Ratio of catches per 10 hours fishing of research to commercial trawlers

Year Class	1950	1949	1948	1947	1946	1945	1944	1943+
1950...	—	4·19	0·79	0·38	0·12	0·17	0·19	0
1951...	10·32	0·57	0·20	0·09	0·14	0·14	0·14	0

It should be noted that much of this section forms the dual to similar work by Beverton and Holt (in press), who approached the problem from the opposite side, in estimating the mortality caused by a known amount and distribution of fishing. If the catch is known, of course the knowledge of one of either the abundance or the fishing mortality implies a knowledge of the other. In the same way as density and abundance are here distinguished, density being the dominant one, so they use fishing effort, and fishing intensity—effort per unit area—intensity being the

more important. The general similarity of approach is most obvious in dealing with the concentration, where it will be shown that our equation (2.4) for overall density is virtually the same as their expression for overall fishing intensity. Symbolically the various relations discussed may be expressed as follows :

Y = catch of fish, in numbers, in the region considered
A = area of the region
F = fishing mortality coefficient
f = fishing intensity
g = fishing effort
d = catch per unit effort
D = density of fish
N = abundance of fish

and the relations below follow directly

$$FN = Y = gd$$

$$f = \frac{g}{A} \qquad D = \frac{N}{A}$$

Then the basic assumption made by Beverton and Holt may be expressed as

$$F = cf$$

while the assumption used in this paper is

$$d = c' D$$

where c' is a constant provided the availability is constant. These two assumptions are really the same for

$$c = \frac{F}{f} = \frac{Y}{N} \div \frac{g}{A} = \frac{Y}{N} \div \frac{Y/d}{N/D} = \frac{d}{D} = c'$$

Concentration of fishing in space and time

The concentration of the fishing fleet on the fish is the factor which is most easily estimated, and hence corrected for, provided sufficiently detailed information is available. Without such correction a shift in the fishing effort, either by commercial or research vessels, say from an area of low density to one of high density, thus giving a greater catch, would appear as a greater c.p.e. (catch-per-unit-effort), and hence as an apparent increase in the density. For instance, suppose there are two areas of markedly different densities ; in one the catch per hour is 100 fish, in the other only 10 fish. Suppose also that in one year 30 hours fishing is done in the first area but 70 hours in the second, e.g., because of presence there of some other favoured species, but that these figures are reversed the following year. Then in 100 hours fishing $30 \times 100 + 70 \times 10 =$ 3,700 fish are caught in the first year, but $70 \times 100 + 30 \times 10 = 7{,}300$ fish in the second, which would appear to indicate a doubling in density between the two years.

If the whole region is divided into a number of separate sub-areas, the c.p.e. within each will be less dependent on the concentration than is the c.p.e. of the entire region, and a more reliable density index is then obtained by averaging the separate indices for each sub-area. With sufficient information the sub-division could be continued until the c.p.e. in each sub-area is independent of the concentration, and hence a density index obtained free from variations in the concentration, and depending only on the vulnerability and aggregation. This method cannot be extended to estimate and correct for the aggregation, for it depends essentially on having some index of density, and therefore some fishing, in each sub-area used, over intervals of time so short that there is effectively little change in density within any sub-area. This is possible for reasonably large sub-areas, but the estimation of the aggregation needs the fine sub-division of an area of only a few miles square, and over a short time, and it is extremely unlikely that fishing will take place in all sub-areas.

The correction for the concentration, which is fundamentally merely another example of stratified sampling, may be expressed mathematically as follows. Let the region be sub-divided into m sub-areas, in each of which the density is assumed proportional to the catch-per-unit-effort, i.e.

$$d_i = c_i D_i \qquad i = 1, 2, \ldots\ldots m$$

where D_i = density in i^{th} sub-area

d_i = c.p.e. in i^{th} sub-area

c_i = constant = reciprocal of vulnerability × aggregation

and if A_i = area of i^{th} sub-area

N_i = number of fish in i^{th} sub-area

and similar terms without the sub-script denote the value for the whole region

$$\text{then} \quad N_i = A_i D_i \qquad N = AD$$

$$\text{and} \quad N = \sum N_i = \sum A_i D_i \quad \ldots\ldots\ldots\

in 1950 and 1951. As a result (2.6) which is the corresponding equation to (2.4) cannot be deduced from (2.5) by putting all c_j equal,

$$\frac{1}{c}\frac{\sum t_j d_j}{\sum t_j} \neq D \quad \ldots\ldots(2.6)$$

But

$$D = \frac{\sum t_j d_j}{\sum t_j} = \frac{\sum c_j t_j D_j}{\sum t_j} \quad \ldots\ldots(2.7)$$

and the right hand side is not directly dependent on variations in the seasonal distribution of fishing effort. If the values of c_j are the same for corresponding seasons of different years, and the changes in D during the year are the same for each year (i.e. $D_j = k_j D$ where k_j is the same for all years), then (2.7) will provide an index for the year's density, independent of changes in the seasonal distribution of fishing, and which is formally the same as that correcting for changes in the spatial distribution.

$$\text{i.e.} \quad \frac{\sum t_j d_j}{\sum t_j} = \frac{\sum c_j t_j k_j}{\sum t_j} D = \text{constant} \times D \quad \ldots\ldots(2.8)$$

If the effect of the fishery on the stocks is great, then a marked change in the time of fishing will alter the distribution of density throughout the year, e.g., relatively more fishing early in the year will decrease the later density. That is k_j will not be the same in different years when the

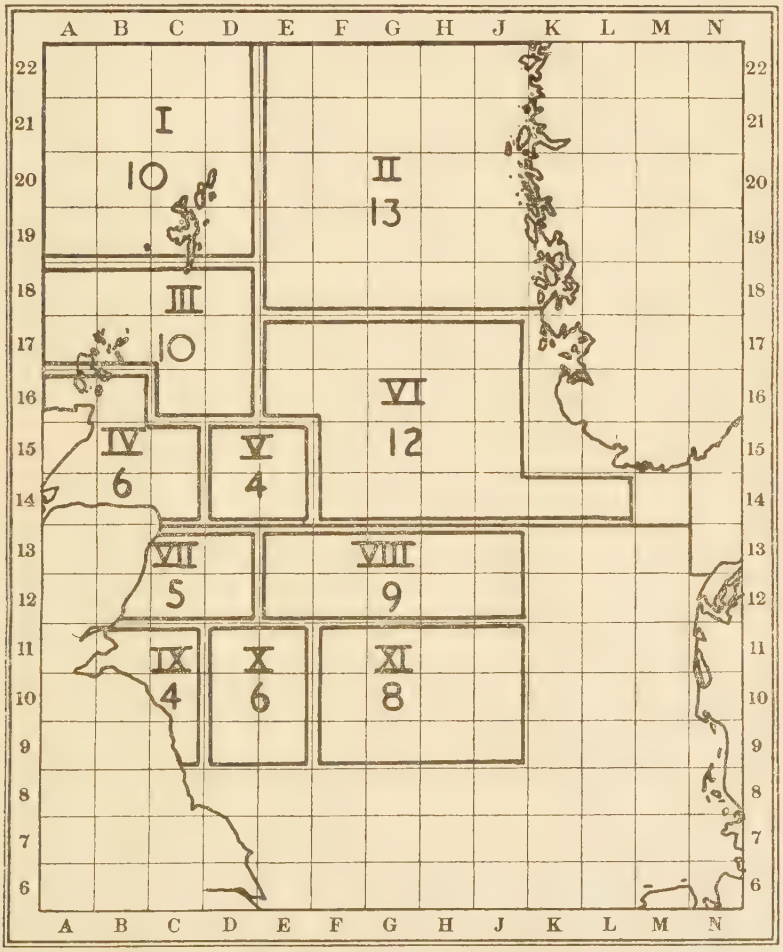

FIG. 2.1. Concentration of fishing on northern North Sea haddock. Chart showing the sub-regions and their arbitrarily chosen areas (lower Arabic figures), used to obtain a density index for haddock free from the effects of concentration.

seasonal distribution of fishing is different. In such cases there is no single figure which is a completely adequate measure of the density for the whole year, and (2.8) provides a figure which is as satisfactory as any.

The type of improvement achieved by dividing the period and area in which a fishery takes place into smaller and more homogeneous sub-areas may be seen by analysing month by month the data of the British haddock fishery in the northern North Sea during 1951 and 1952. The haddock is a suitable fish for this type of analysis because there are marked seasonal changes in its geographical position, which are followed—with fair accuracy—by the distribution of the fleet. Information is available in the form of catches and number of hours fishing in each statistical rectangle. As fishing was not carried out in each rectangle during each month, the North Sea north of 55°N had to be divided into 11 areas, each containing 4 or more rectangles. These areas were chosen by two criteria—that there had been fishing in them in each month of the year, and a relatively uniform distribution of haddock within each ; it is not suggested that the precise sub-regions chosen are by any means the best, and actually they do not fulfil even the first criterion exactly. In using (2.4) the value of A_i, the area of each sub-region, was difficult to define exactly for the sub-regions touching the coast, and for those on the north and west of the whole region, lying on the edge of the distribution of the British fishing. The somewhat arbitrary areas used are shown in Fig. 2.1.

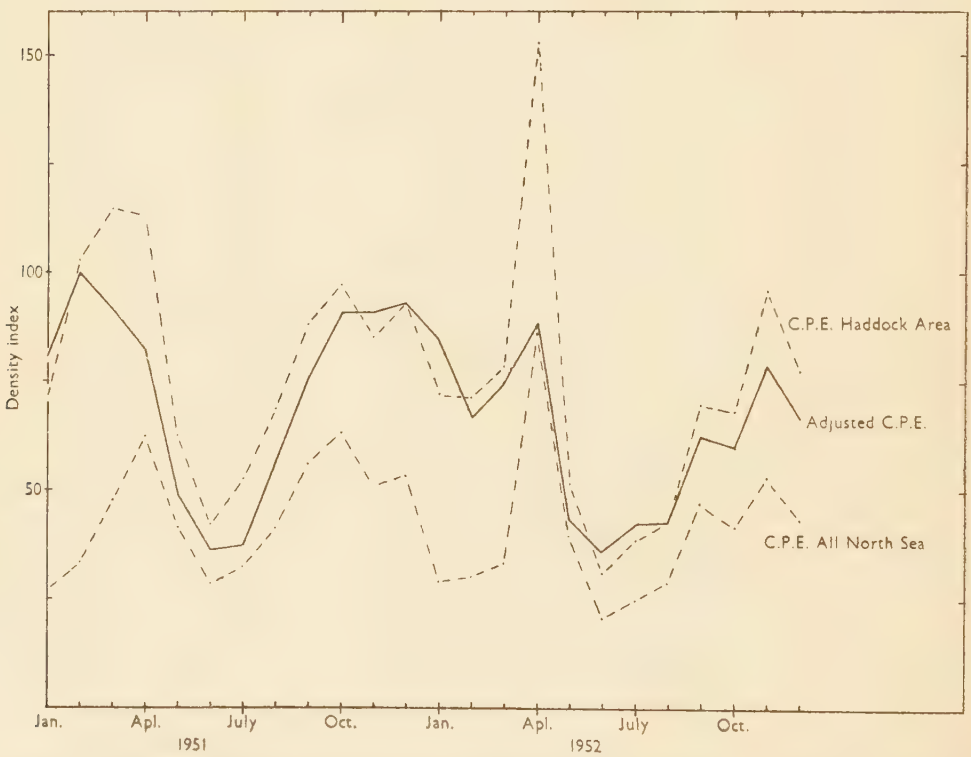

FIG. 2.2. Density indices for North Sea haddock as determined by three different methods.

From the calculations, three indices of haddock density are available for each month. (1) The catch-per-effort over the whole North Sea. (2) The catch-per-effort in the 'haddock area' north of 55°N. (3) The density index using (2.4). These have been plotted in Fig. 2.2.

The general shape of all three curves is much the same, with the c.p.e. in the whole North Sea being about two-thirds of the height of the other two. A closer comparison of these latter shows that for most months, particularly in the second half of each year, the simple c.p.e. is some

5 per cent above the corrected figure, indicating a small and relatively constant degree of concentration of the fleet on the haddock. In other months, April 1952 being the best example, the c.p.e. has extreme values, and is not followed at all closely by the corrected density. In the early spring this is due to the fishery on the spawning fish when the fleet is concentrated on the haddock to a much greater degree than in the rest of the year, giving an artificially inflated catch-per-unit-effort. At other times the fleet is less concentrated than normal and the c.p.e. is artificially reduced, even falling below the adjusted density in June–July, 1952. The overall impression from the figure is that the indices of density follow each other reasonably closely, but that the extremes in the simple c.p.e. have been flattened out in the corrected value. The numerical value of the concentration, as defined on page 30, for the haddock area, may be obtained as the ratio of indices (2) and (3). It varies between 0·85, for January, 1952 and 1·72 in April, 1952.

In default of any knowledge of the true density of haddock in each month, it is impossible to give a direct measure of the improvement, if any, achieved by dividing up the region. An indirect measure can be gained by a comparison of the variability of the indices. In doing this the logarithms of the indices have been used, rather than the indices themselves, because the two indices may differ in their means, but their percentage variability should be the same. The variances of the logarithms of the two density indices for the area north of 55°N have been calculated and are 0·0271 for the catch-per-effort and 0·0209 for the adjusted density. Each of these terms is the combination of the variance of true density and the errors made in its estimation, and unless there is a systematic tendency to over-estimate the lower densities and to under-estimate the higher densities, the estimated variance will be greater than the true variance by an amount depending on the errors. Thus the difference in the variance of the two indices is a measure of the difference in accuracy and, allowing for the variance of the true density, it is probable that the 25 per cent reduction in variance using the adjusted density represents reduction of the error variance by up to $\frac{1}{2}$. That is, the adjusted figure may be up to twice as accurate as the raw c.p.e. Even in the adjusted figure there are marked divergences from the probable true density, particularly in the spring. For example, the apparent June 1952 density is only 41 per cent of that in April (compared with only 20 per cent for the raw c.p.e.) ; while a more probable value would be between 70 and 90 per cent. The divisions used are therefore probably too large, though it is also possible that the constant c of (2.2) is greater for the shoals of spawning haddock off the Shetlands due to the greater aggregation.

These calculations can also serve to illustrate the effect of variations in time. In Table 2.4 are shown the densities in each of the eleven sub-areas in 1952 ; in the first row as the c.p.e. for the year as a whole and in the second as the mean c.p.e. of each month.

TABLE 2.4

Indices of yearly haddock density for separate sub-areas of the North Sea, 1952

Area	1	2	3	4	5	6	7	8	9	10	11	Total
Year's c.p.e.	119	90	62	52	36	61	71	58	68	61	25	68·9
Mean monthly c.p.e. ..	100	89	70	53	37	55	62	48	52	58	22	71·0
% difference	+19	+1	−11	−3	−1	+10	+15	+20	+33	+6	+15	−3

There are considerable differences between the two figures for density within each area, and also, what is in some ways more important, these differences vary very greatly from area to area. Thus, while in most of the areas the yearly figure is up to 33 per cent greater than the mean monthly c.p.e., in area 3 it is 11 per cent smaller. This causes serious errors when comparing the density in two different areas, for instance, by taking the year as a whole, area 9 appears to have a slightly denser haddock population than area 3, but the mean of the monthly figure —a more reliable index— shows that the haddock density in area 3 is about 35 per cent greater. This effect is because in each month the trawlers naturally collect in the areas of highest density, so that within each area

the fishing is greatest in the months of greatest density, though this simple connection breaks down in many areas because trawlers collect there for other species besides haddock, e.g., cod and coalfish.

Standardization of Fishing Effort

To obtain a reliable index of density from the operations of a commercial fleet requires that the unit of effort should be standardized. This need arises equally when estimating the mortality caused by a fleet's activities, and has been discussed by Beverton and Holt (in press), and the treatment below follows theirs closely, though from a different point of view. Ideally a unit of effort should be such that it will represent the same average effective amount of fishing at any place or time ; i.e. the ratio of catch-per-unit-effort to density should be constant. Thus the simple number of units of gear in use will give an unreliable measure of effort if there is any change in the average duration of use. The effort in present English statistics is given in terms of hours fishing, days absence or number of trips of trawlers. Of the three, the first is the best form, as it refers directly to the amount of fishing done and allows for loss of time going to and from the fishing grounds, and due to bad weather. However, because some ships are larger and more powerful than others, 100 hours fishing by a large ship may represent a greater effective amount of fishing than 200 hours by a smaller ship. Thus, if simple hours fishing were used as the index of effort, the index of density as given by the catch-per-unit-effort would be twice as great in an area fished by the larger vessels, as in an area of the same true density but fished by smaller ships. This may well have serious results, as in many fisheries large and small ships tend to fish in different areas, or there may be a definite change in average size of ship with time. This has to be corrected by using a measure of effort which is more closely related to the true amount of fishing. Ideally the fishing power of every ship could be estimated by comparison of its catches with those of other ships fishing at the same time and place, all ships being finally referred to a single standard vessel. This last could well be a special research vessel, whose fishing power could be held constant over a period of years. The effort expended by each vessel could then be expressed in the product of its fishing power and duration of fishing ; the effort of the fleet is then the sum of the effort of all the ships. The calculation of fishing power for each ship would be a very lengthy process, especially as the estimates would be highly variable unless the catches of a number of trips of each ship were used. However, the main purpose would be achieved if the power of any ship could be estimated from its specifications, so as to eliminate the serious systematic errors between large and small ships caused when the simple number of hours fishing is used as the index of effort. Beverton and Holt showed that for English North Sea trawlers the fishing power, as determined from the comparisons of catch-per-unit-effort of ships fishing on the same grounds, is almost proportional to the gross tonnage. This relation holds separately for both steam and motor trawlers, though the factor of proportionality is different for the two types of propulsion, the factor for motor trawlers being 1·4 times that for steam trawlers. If the fishing effort is expressed in terms of the product of gross tonnage and hours fishing, and the motor trawler effort is increased by a factor of 1·4, then the resulting expression of 'steam-trawler-ton-hours' will be a consistent measure of effort. That is, a million 'steam-trawler-ton-hours' will represent the same average effective amount of fishing whether it is done by a few large trawlers, or many small ones. A consistent index of effort can be found by similar methods in other types of fishing.

Even when the effort is given in the form, say, of steam-trawler-ton-hours, it may still be unreliable because the effective effort may alter with changes in the density of fish stocks. While this change in fishing power is probably small or non-existent in the trawl, it can be large in other types. Generally, if there is a change it will appear as a falling off in efficiency due to increasing saturation of the gear, and the instantaneous fishing power of the gear will be determined by the amount so far caught. If the form of this dependence can be established, then from a knowledge of the actual catch an estimate can be made of the average effective effort exerted by the gear while in operation. Hence an adjusted catch-per-unit-effort can be calculated and a true index of population density determined. Long-line fishing is particularly amenable to mathematical treatment along these lines. Assuming that the fishing power is proportional to the number of unoccupied hooks, the mean effort for any catch is readily calculated.

Let n = total number of hooks
y = instantaneous rate of capture per hook
Y_t = total catch up to time t, in numbers

$$\therefore \frac{dY_t}{dt} = \text{rate of capture} = y(n - Y_t) \quad \ldots\ldots(2.9)$$

$$\therefore -\log(n - Y_t) = yt + \text{constant}$$

$$\therefore Y_t = n(1 - e^{-yt}) \quad \ldots\ldots(2.10)$$

This equation is identical with (8.40) of Beverton and Holt, who have given a long discussion on the general problem of gear saturation.

If f_T = average effort exerted between $t = 0$ and $t = T$,

$$f_T = \frac{1}{T}\int_o^T (n - Y_t)\,dt$$

$$= \frac{1}{T}\int_o^T n\,e^{-yt}\,dt$$

$$\therefore f_T = \frac{n}{yT}(1 - e^{-yT}) \quad \ldots\ldots(2.11)$$

$$\text{or } f_T = \frac{n \,.\, Y_T}{yT \,.\, n}$$

This is conveniently expressed in terms of p, the proportion of occupied hooks at time T, $= \frac{Y_T}{n}$

From (2.10) we have $yT = -\log\left(1 - \frac{Y_T}{n}\right)$

$$\therefore f_T = -\frac{Y_T}{\log\left(1 - \frac{Y_T}{n}\right)}$$

$$= \frac{-np}{\log(1 - p)} \quad \ldots\ldots(2.12)$$

(2.11) can also be written in the form

$$f_T = \frac{Y_T}{yT}$$

$$\text{or } \frac{Y_T}{f_T T} = \frac{nyT}{nT} \quad \ldots\ldots(2.13)$$

Now nyT is the catch which would be obtained if no saturation of gear had taken place, so that the right-hand side of (2.13) is the expected catch-per-unit-effort with no saturation, while the left-hand side is the catch divided by the adjusted effort. The adjustments have therefore had the desired effect of producing an index of density undistorted by gear saturation.

These results are shown graphically in Fig. 2.3 in which the effective effort and the corrected catch-per-unit-effort are plotted against p, the proportion of occupied hooks. The effective effort falls steadily and extremely rapidly when most of the hooks are occupied, while the adjusted catch-per-unit-effort, i.e. the estimated density, increases rapidly. The graph can be used to read off the estimated density for any catch and effort. Suppose a line of 1,000 hooks is put down for one night and that the unadjusted effort may be expressed as 1,000 hook-nights, and the catch is 350 fish. Then 35 per cent of the hooks are occupied, and from the graph this gives an average effort equal to 82 per cent of possible. Then the adjusted effort is 820 hook-nights and the density 430 fish per 1,000 hook-nights.

Properly, these calculations will hold only when the fish are liable to be caught at a constant rate and move independently. If the fish move in a shoal, then one part of the line, where the shoal passes it, may be quickly saturated, while the rest of the hooks are unoccupied. Again the fish may tend to spread out in separate territories and the fact that one hook catches a fish will not reduce the catching power of the line, as there are no more fish within the range of the hook.

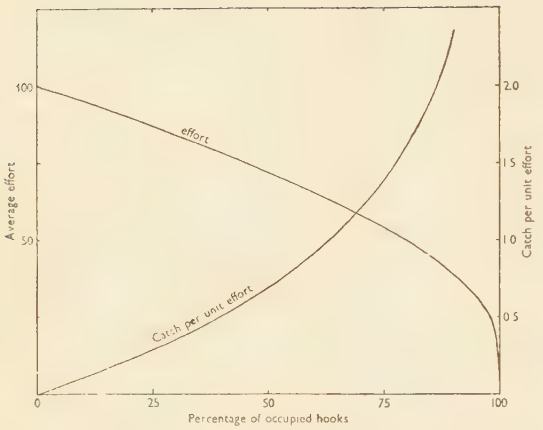

FIG. 2.3. Effort and catch-per-unit-effort in an idealized long-line fishery, showing the effect of gear saturation.

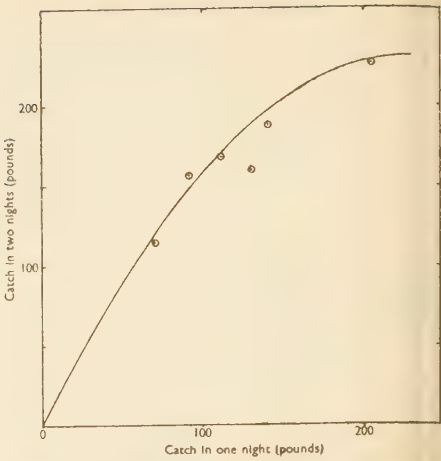

FIG. 2.4. Theoretical curve and observed points, relating catch of gill nets lifted after one and two nights, showing the effect of gear saturation.

The correction applied will be too small in the first case and too large in the second. Strictly, too, the calculation only holds for one set of hooks in a uniform density of fish, not for a large number of sets, e.g., a fleet's operation, which will be in varying densities of fish. However, if applied to a fleet's operations, using the average proportion of hooks occupied, the formulae do provide a method whereby the catches from line fishing can be used to give a relatively unbiased estimate of stock density.

Similar calculations can be used for other types of gear where saturation is effective. A noticeable example has been given by Kennedy (1951), in the gill-net fishery in the Great Slave Lake. He compared the catches from nets lifted daily and those lifted at intervals of two or more days and noted that the nets became 'saturated' with a catch of about 230 pounds. This is analogous to a line of 230 hooks each capable of taking a one-pound fish, though the analogy breaks down in exceptional cases of 'super-saturation', when up to 400 pounds were caught, due probably to a large shoal of fish being caught at the same time. Using (2.10) we can put $n = 230$ lb., and get for the catch after one and two nights—

$$Y_1 = 230\,(1 - e^{-y})$$
$$Y_2 = 230\,(1 - e^{-2y})$$

Plotting $230\,(1 - e^{-y})$ against $230\,(1 - e^{-2y})$ for values of y, the density of fish, gives a graph of the catch expected from two nights' fishing, against the catch from one night ; this is shown in Fig. 2.4. Kennedy, in Table I, p. 267, gives, for six different areas, the average catches from one and two nights and these six points are plotted on the graph. These points fit the line very well, giving a good measure of support to the theoretical model.

Sampling of Fishing Effort

In many fisheries, particularly those carried out by small ships from many separate fishing ports, accurate statistics of the whole of the fishing effort and its distribution cannot readily be obtained.

However, as suggested earlier, it is not necessary to use the whole of the commercial fishing to obtain adequate estimates of the catch-per-effort, and for a large fishery the sample need only be a small fraction of the total. To illustrate this, samples have been taken from the records of the trawler landings at Lowestoft in January and July, 1951. These records consist of a form for each ship landing, recording the ship's catch, the time spent fishing, and the fishing ground.

In practice, it is likely that the sampling system would be a collector covering several ports visiting each in turn ; thus at each port, all vessels landing on certain days would be sampled

but none on other days. To correspond with this, each morning's landings in the two months has been chosen as a separate sample rather than attempt to take truly random samples from the whole month's landings. That is, each sample consists of information on the fishery activities of all boats landing on one morning ; these activities will generally extend over some 10–12 days previous ; the samples will not refer to all fishing on one particular day. In January when the month's catch averaged 1·13 cwt. per hour fishing, the estimates from individual mornings ranged between 0·99 and 2·05. In July, the month's catches averaged 0·96 cwt. per hour fishing and the estimates from individual mornings ranged between 0·78 and 1·27. The large value of 2·05 in January is due to a morning when only four boats landed, instead of the average of 10–12 boats, and all these happened to have very good catches. Apart from this, and another morning with only 3 landings, for which the average was 1·70 cwt. per hour fishing, the range in January is only from 0·99 to 1·29 cwt. per hour.

Thus, by sampling only one morning a month, i.e. roughly $\frac{1}{25}$ of the total, an estimate of the catch-per-unit-effort is obtained which is unlikely to depart from the true value by more than about 20 per cent. When the average c.p.e. is taken over the year, or from a number of different ports, this accuracy is probably adequate for most purposes, but of course improved accuracy can be obtained by intensifying the sampling. For instance, instead of taking samples once a month, they are taken from every seven days (excluding Sundays), then the 7 possible estimates of the c.p.e. for January range between 1·09 and 1·16, and for July between 0·84 and 1·09.

This sampling of the fleet can also be used to obtain estimates of the total effort and its distribution, particularly if the total catch is known. Then the sample catch is a known fraction of the total catch, and the effort is easily found on the assumption that the sample effort is the same fraction of the total. This is in effect assuming that the catch-per-unit-effort is the same for the sample and the total. Alternatively, if the total catch is not known, the total effort might be estimated on the assumption that the effort expended is the same for each day's landings. For example, if samples are taken every 10 days, the total effort is estimated as 10 times the sample effort. At Lowestoft and other English ports this latter assumption is far from being true. The number of ships landing varies considerably, and in a non-random manner, during the week, with particularly low landings on Fridays. This could give a considerable bias if samples tended to be collected on particular days of the week ; if all samples were taken on Fridays, the effort estimated with the second assumption would be under-estimated by some 50 per cent. This bias is eliminated with the first method, which also, at least for Lowestoft gives much less variable results. There could well be fisheries, however, for which the second assumption is the better ; such is one where the boats only go out for a few hours returning each day, so that the effort is nearly constant each day, though the catch and hence the catch per effort may vary considerably. Bias is again possible here, certain days of the week being more popular than others.

The effort in any particular area can be estimated in a similar way as the total effort, though naturally the estimates will be more variable, particularly for areas where only a few fishing trips were made.

These methods can be described simply in mathematical terms.

Let C = total catch
E = total effort
N = total number of days in relevant period
c = sample catch
e = sample effort
n = number of days on which samples were taken
e' = sample effort in a particular area

Then, for the first assumption

$$\frac{c}{e} = \text{catch per effort}$$

$$E_1 = e \,.\, \frac{C}{c} = \frac{C}{c/e} = \text{total effort}$$

$$E_1' = e' \frac{C}{c} = \text{total effort in particular area}$$

and for the second assumption,

$$E_2 = e \cdot \frac{N}{n} = \text{total effort}$$

$$E_2' = e' \cdot \frac{N}{n} = \text{total effort in particular area}$$

The results of applying these methods to the Lowestoft landings of January and July, 1951, are shown in Tables 2.5 and 2.6. Table 2.5 shows for each month, and method, and for each of two sampling intensities, the extreme upper and lower estimates for the month's effort, the mean estimates and the standard deviation. For method 1 the results are of course the same as for the estimates of the catch-per-unit-effort, being within about 20 per cent for the single days' sampling, with two extreme values in January, and the estimates for the more intensive sampling being extremely close. For method 2 the estimates are much more scattered.

TABLE 2.5

Estimates of total hours fishing by Lowestoft trawlers in January and July, 1951

Month	January		July	
True Effort	35,376		29,974	
Samples per Month	1	3–4	1	3–4
Lowest Estimate (1)	19,466	34,388	22,648	26,337
Mean Estimate (1)	34,819	35,376	30,449	30,316
Highest Estimate (1)	40,353	36,588	36,800	34,024
Lowest Estimate (2)	6,760	22,952	4,602	21,099
Mean Estimate (2)	35,376	35,832	29,974	30,045
Highest Estimate (2)	56,264	47,832	48,802	36,816
Standard Deviation (1)	4,700	834	3,393	2,644
Standard Deviation (2)	15,639	9,256	12,625	5,735

TABLE 2.6

Estimates of hours fishing in different areas (statistical rectangles given) by Lowestoft trawlers, 1951

Sample \ Area	1 E–G 1–5	2 H–J 1–5	3 C–G 6–15	4 H–M 6–15	5 Outside Region IV
JANUARY					
1	24,359	—	—	12,010	—
2	20,540	—	—	16,048	—
3	27,456	—	—	7,260	—
4	25,438	—	—	9,417	—
5	27,458	543	—	7,491	—
6	23,589	—	—	11,632	—
7	17,596	—	—	16,792	—
True Effort	24,106	105	—	11,165	—

	JULY				
1	12,032	620	9,203	7,035	625
2	16,391	—	5,391	12,241	—
3	16,560	2,160	3,137	11,531	—
4	13,036	725	8,406	4,589	2,103
5	11,614	—	7,949	9,866	587
6	11,511	—	9,796	8,715	51
7	5,816	1,305	4,253	14,963	—
True Effort	12,178	646	7,245	9,283	622

Table 2.6 shows the effort in 5 different areas, as estimated by method 1 and sampling every days. The estimates of the effort in the heavily fished areas (1 and 4 in January, and 1, 3 and 4 ı July) are reasonably accurate, and though the exact value of the effort in other areas is not stimated very well, this degree of sampling enables them to be distinguished as areas of little shing. More important, any appreciable change in the distribution of the fleet can be detected, ıe differences between the January and July distributions being very apparent from a comparison f any pair of samples, one from each month.

This example shows that at Lowestoft the catch-per-unit-effort and the total effort and its istribution can be adequately estimated by sampling only one-seventh of the landings. The action of the total needed to give equally satisfactory estimates will of course not be the same ır all fisheries, the dominant factors being the general variability of the landings and their total ımber. Naturally the more similar is the catch-per-effort of different boats, the smaller will e the necessary sample. For a certain variability, a given percentage accuracy will in general be ɔtained by a sample size of a fixed number of landings, rather than a fixed fraction of the total. hus the larger Lowestoft samples are of about 20–30 landings, which gives a fair guide to the ze of sample needed for the same accuracy in similar fisheries. The smaller samples (one day's ndings) were from 3 up to 17 landings. As indicated, 3 or 4 landings formed too small a sample ıd gave some extreme estimates, but samples of half-a-dozen landings gave useful estimates.

ge-composition

In the previous sections methods have been deduced of obtaining indices of density free from veral sources of variance. This density, however, has so far only been in terms of total weight numbers of a certain species of fish, or rather, more strictly, weight of all fish above the selective nge of the gear in use. It is usually also important to have separate density indices for each e of fish. If the age-composition of all commercial samples is substantially the same, for all nes or places of capture, then this presents no problem. The observed age-composition of the tches can be applied directly to the density index for all fish to give the desired index. Thus he index for all fish is 100, and in the catches 10 per cent are say, four years old, then the required lex for four-year-old fish is $100 \times 0{\cdot}1 = 10$. When, as in the North Sea plaice, the situation simple enough for the total catch divided by the total effort (say hours fishing), to be an appro- ate density index for all fish, then density indices for each age are most easily obtained by iding the number landed of that age by the total effort. For the plaice of the southern North ı the results of doing this are shown in Table 3.1, which gives the number caught in each 100 urs fishing by Lowestoft trawlers.

When the age-composition is not the same for all sub-divisions of the catch, then methods ılogous to those of the previous section will have to be used for each age separately. Thus, lifferent ages occur in different parts of the fishing region, this region will have to be divided ɔ a number of sub-areas each of which is homogeneous as regards age-composition—these ll almost certainly be larger than those needed to give a homogeneous density. In each of these -regions density indices, firstly for the species, and then for each age separately, may be deter- ıed, and then combined to give density indices for the complete region. Similar methods can used for changes in age-composition with time during the year.

PART III

ESTIMATION OF POPULATION PARAMETERS

Growth Rate

Provided that the age of individual fish can be determined, the growth rate presents few problems, and normally can be calculated with a much greater accuracy than the mortality rates. If random samples from the catch are taken for age determination, then of course the average weight, or length, of fish of a given age in the sample gives an estimate of the average weight at this age in the sea, which will be unbiased provided the length distribution of the catch is the same as that of the natural population. Bias is likely among the youngest fish, which are not fully fished and among which the largest and fastest growing are likely to be over-represented in the catch.

The samples taken for age determination in the North Sea plaice are, as suggested in Part II, not completely random. Within each 5-cm. group samples are taken randomly, but the number taken in each group are pre-determined, and give an over-representation of the larger fish. Hence in the whole sample the average size of a given age will tend to be greater than the true value. This is easily corrected by taking the mean size of a given age within each 5-cm. group, and taking the weighted mean over all size-groups, the weighting factor being the number of fish of the given age in each length-group. That is, using the notation of Part I,

$N_i p_i$ = number of fish of age t in i^{th} length-group

w_i = mean weight of fish of age t in i^{th} length-group

and if W = mean weight of fish of age t

$$\text{then } W = \frac{\sum N_i p_i w_i}{\sum N_i p_i} \quad \text{.....(3.1)}$$

For random sampling the variance of the weight at a given age may be assessed directly, but for stratified sampling it is given by adding the contributions from each length-group.

If σ_i^2 = variance of weight at age t within the length-group

and σ^2 = total variance of weight at age t

$$\sum N_i p_i \sigma^2 = \sum N_i p_i \left\{\sigma_i^2 + (W - w_i)^2\right\} \quad \text{.....(3.2)}$$

In practice the variance of weight at age t is generally so small for either method that there is no need to reduce it by refinements of the sampling system, which will be designed rather to obtain the greatest accuracy for the age-density indices, and hence for the mortality estimates.

Mortality

The total mortality may be best expressed as an instantaneous rate, but may be expressed as the percentage of fish dying in one year, or as the percentage surviving to the next year.

If M = instantaneous mortality rate

then $1 - e^{-M}$ = fraction dying in one year = $1 - S$

e^{-M} = fraction surviving to the next year = S

Once indices of density of each age of fish, or at least of those above the selection range of the gear in use, have been calculated for two successive years of observation, estimates of mortality rates are easily made.

If ${}_1n_x$ = density index for fish age x in 1st year

${}_2n_{x+1}$ = density index for fish age $x + 1$ in 2nd year i.e. the same year-class

and m_x, s_x are the estimated mortality and survival rates for fish aged x

$$\text{then } s_x = \frac{{}_2n_{x+1}}{{}_1n_x} \quad \text{.....(3.3)}$$

$$m_x = log\ {}_1n_x - log\ {}_2n_{x+1} \quad \text{.....(3.4)}$$

lso if ${}_1N_x$, ${}_2N_{x+1}$, M_x, S_x are the true densities and mortalities,

$$S_x = \frac{{}_2N_{x+1}}{{}_1N_x} \quad \text{.....(3.5)}$$

$$M_x = log\ {}_1N_x - log\ {}_2N_{x+1} \quad \text{.....(3.6)}$$

should be noted that these estimates of mortality, unlike those based on catch curves (see Ricker 948), or percentage age-composition, are free from distortion due to varying strength of year-classes.

To estimate the variance and possible bias of the mortality and survival estimates we will suppose

$${}_1n_x = k_1N_x\,(1 + {}_1\varepsilon_x)\ ;\ {}_2n_{x+1} = k_2N_{x+1}\,(1 + {}_2\varepsilon_{x+1})$$

where k is a constant depending on the density index used and ${}_1\varepsilon_x$, ${}_2\varepsilon_{x+1}$ re random variables equal to the error in the density estimates ; if there is no bias they will ave mean zero. If the variances of ${}_1n_x$, ${}_2n_{x+1}$ are $k^2\ {}_1N_x{}^2\ {}_1\sigma_x{}^2$, $k^2\ {}_2N_{x+1}{}^2\ {}_2\sigma_{x+1}{}^2$ respectively, the ariances of ${}_1\varepsilon_x$, ${}_2\varepsilon_{x+1}$ are ${}_1\sigma_x{}^2$, ${}_2\sigma_{x+1}{}^2$ which will be assumed to be small.
herefore from equation (3.4), $m_x = log\ {}_1n_x - log\ {}_2n_{x+1}$

$$= log\ {}_1N_x + log\,(1 + {}_1\varepsilon_x) - log\ {}_2N_{x+1} - log\,(1 + {}_2\varepsilon_{x+1}) \quad \text{.....(3.7)}$$

ow using the identity, $\log\,(1 + y) = y - \frac{1}{2}\,y^2 + \frac{1}{3}\,y^3 + \ldots\ldots$ for $|y| < 1$ nd ignoring terms smaller than ${}_1\varepsilon_x{}^2$ the equation becomes

$$m_x = log\ {}_1N_x - log\ {}_2N_{x+1} + \left\{{}_1\varepsilon_x - \tfrac{1}{2}\ {}_1\varepsilon_x{}^2\right\} - \left\{{}_2\varepsilon_{x+1} - \tfrac{1}{2}\ {}_2\varepsilon_{x+1}{}^2\right\}$$

$$\therefore m_x = M_x + {}_1\varepsilon_x - {}_2\varepsilon_{x+1} - \tfrac{1}{2}\left\{{}_1\varepsilon_x{}^2 - {}_2\varepsilon_{x+1}{}^2\right\} \quad \text{.....(3.8)}$$

On the right hand side of this equation, the mean values of ${}_1\varepsilon_x$ and ${}_2\varepsilon_{x+1}$ are zero for an nbiased estimate of density and the mean of $\left\{{}_1\varepsilon_x{}^2 - {}_2\varepsilon_{x+1}{}^2\right\}$ being the difference of two small rms, which are likely to have nearly the same mean, will be very small. Therefore the mean lue of m_x is M_x. That is, m_x is approximately an unbiased estimate of M_x.

The variance of m_x = Expectation of $(m_x - M_x)^2$
(see Kendall (1947), p. 84)

$$= E\,(m_x - M_x)^2$$

$$= E\,({}_1\varepsilon_x - {}_2\varepsilon_{x+1})^2 + \text{smaller terms}$$

$$= E\,({}_1\varepsilon_x{}^2 - 2\ {}_1\varepsilon_x \cdot {}_2\varepsilon_{x+1} + {}_2\varepsilon_{x+1}{}^2)$$

s ${}_1\varepsilon_x$, ${}_2\varepsilon_{x+1}$ are the errors made in different years they will be independent and hence

$$E\,({}_1\varepsilon_x \cdot {}_2\varepsilon_{x+1}) = 0$$

$$\therefore \text{variance } m_x = {}_1\sigma_x{}^2 + {}_2\sigma_{x+1}{}^2 \quad \text{.....(3.9)}$$

an exactly similarly way we have

$$s_x = \frac{{}_2n_{x+1}}{{}_1n_x} = \frac{{}_2N_{x+1}\,(1 + {}_2\varepsilon_{x+1})}{{}_1N_x\,(1 + {}_1\varepsilon_x)}$$

$$= S_x\,(1 + {}_2\varepsilon_{x+1})\,(1 + {}_1\varepsilon_x)^{-1} \quad \text{.....(3.10)}$$

d expanding,

$$s_x = S_x\,(1 + {}_2\varepsilon_{x+1})\,(1 - {}_1\varepsilon_x + {}_1\varepsilon_x{}^2) \text{ ignoring powers of } \varepsilon \text{ above 2}$$

$$= S_x\,(1 + {}_2\varepsilon_{x+1} - {}_1\varepsilon_x + {}_1\varepsilon_x{}^2 - {}_1\varepsilon_x\ {}_2\varepsilon_{x+1} + {}_1\varepsilon_x{}^2 \cdot {}_2\varepsilon_{x+1})$$

$$\therefore E\,(s_x) = S_x\,(1 + {}_1\sigma_x{}^2) \quad \text{.....(3.11)}$$

his means that s_x is biased, having a mean higher than the true value S_x. The amount of bias epends on ${}_1\sigma_x$, the coefficient of variation of ${}_1n_x$; for a coefficient of variation of 30 per cent, ${}^2 = 0{\cdot}09$, giving a positive bias of 9 per cent, but for a coefficient of variation of 10 per cent, $_x = 0{\cdot}01$ and the bias is only 1 per cent.

The variance of s_x can also be calculated, and is equal to

$$E\left\{s_x - S_x\,(1 + {}_1\sigma_x{}^2)\right\}^2$$

$$= E\ S_x{}^2\,({}_2\varepsilon_{x+1} - {}_1\varepsilon_x)^2 \text{ ignoring powers of } \varepsilon \text{ above 2}$$

$$\therefore \text{variance of } s_x = S_x{}^2\,({}_2\sigma_{x+1}{}^2 + {}_1\sigma_x{}^2) \quad \text{.....(3.12)}$$

The mortality from one year to the next can be estimated from a number of different year classes ; provided there is no obvious change of mortality with age, as may be seen by inspection of the different values, those may be combined to give a mean mortality for the year. Two ways of doing this are to take the mean value of m for all fully represented ages ($= \bar{m}$, say) or to take the value of m for all the fully represented ages taken together ($= m'$, say).

That is, if $x = 1, 2, \ldots\ldots k$ are the ages for which mortality rates can be determined,

$$\text{then } \bar{m} = \frac{1}{k} \sum_{1}^{k} m_x \quad \ldots\ldots\ldots\

and similarly $E(\beta^2) = \dfrac{\sum {}_2N_{x+1}{}^2 \cdot {}_2\sigma_{x+1}{}^2}{(\sum {}_2N_{x+1})^2}$

and for assumption (B) ${}_1\varepsilon_x = \varepsilon\ {}_1\sigma_x$ where ε is a random variable, mean 0, variance 1, and is the same for all x.

$$\therefore E(\alpha^2) = \frac{1}{(\sum {}_1N_x)^2} \cdot E\left\{{}_1N_x \cdot {}_1\sigma_x\, \varepsilon\right\}^2$$

$$= \frac{1}{(\sum {}_1N_x)^2} \cdot \left(\sum {}_1N_x \cdot {}_1\sigma_x\right)^2$$

$$\text{and similarly } E(\beta^2) = \frac{1}{(\sum {}_2N_{x+1})^2} \cdot \left(\sum {}_2N_{x+1} \cdot {}_2\sigma_{x+1}\right)^2$$

$$\therefore var_A\, m' = \frac{\sum {}_1N_x{}^2 \cdot {}_1\sigma_x{}^2}{(\sum {}_1N_x)^2} + \frac{\sum {}_2N_{x+1}{}^2 \cdot {}_2\sigma_{x+1}{}^2}{(\sum {}_2N_{x+1})^2} \quad \text{.....(3.18)}$$

$$\text{and } var_B\, m' = \frac{(\sum {}_1N_x \cdot {}_1\sigma_x)^2}{(\sum {}_1N_x)^2} + \frac{(\sum {}_2N_{x+1} \cdot {}_2\sigma_{x+1})^2}{(\sum {}_2N_{x+1})^2} \quad \text{.....(3.19)}$$

Making the same simplifications as for (3.17) we have

$${}_1\sigma^2 \frac{\sum {}_1N_x{}^2}{(\sum {}_1N_x)^2} + {}_2\sigma^2 \frac{\sum ({}_2N_{x+1})^2}{(\sum {}_2N_{x+1})^2} \leqslant var\, m' \leqslant {}_1\sigma^2 + {}_2\sigma^2 \quad \text{.....(3.20)}$$

Comparing this inequality with (3.17), the upper limit is the same, but, using the relation $\sum_1^k N_x{}^2 \geqslant 1/k \left(\sum_1^k N_x\right)^2$, the lower limit of $var\, \bar{m}$ is smaller than that of $var\, m'$, the amount depending on the variability of N_x which will tend to be large. Thus $\bar{m}$ would appear to be a better estimate than m'. This is because, though, with the simplification made, the mortality estimates for each age are all of equal variance, they have, in estimating m' given unequal weights. Most often the mortality rates are not equally accurate, being best for the younger and more numerous ages and this gives an advantage to m' as this estimate gives more weight to these ages.

The density indices for each age-group of plaice in the southern North Sea for each of the three biological years from 1st April, 1950, to 31st March, 1953, are shown in Table 3.1. Because the distribution of both fish and fishing are very stable, the density index used need not be very sophisticated ; the one used being the numbers caught per 100 hours fishing by Lowestoft trawlers.

TABLE 3.1

Catch in numbers per 100 hours fishing of each age-group of Lowestoft plaice

Brood Year \ Age	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII+
1950-51	39	929	2320	1722	389	198	93	95	81	57	94
1951-52	91	559	2576	2055	982	261	152	71	57	60	87
1952-53	142	999	1424	2828	1309	519	123	106	61	40	99

TABLE 3.2

Percentage survival and mortality rates of Lowestoft plaice

Brood Year	Age	VI/V	VII/VI	VIII/VII	IX/VIII	X/IX	XI/X	XII+/XI+
1951-52	Per cent Survival	57·0	67·1	76·8	76·3	60·0	74·1	57·6
1950-51	Mortality	0·562	0·399	0·264	0·270	0·511	0·300	0·552
1952-53	Per cent Survival	63·7	52·9	47·1	69·7	85·9	70·2	67·3
1951-52	Mortality	0·451	0·637	0·753	0·361	0·152	0·354	0·396

From these figures the percentage survival and the exponential mortality rates from one year to the next can readily be calculated. These are shown in Table 3.2, for each year-class older than V ; strictly the last figure is not for one year-class, but is the combined survival for fish age eleven and older to twelve and older. There is no very apparent relation between age and mortality, so an overall mortality may be legitimately calculated. This, in the notation of the previous section, gives, for the two pairs of years, the values $\bar{m} = 0{\cdot}41$, $m' = 0{\cdot}49$ and $\bar{m} = 0{\cdot}44$, $m' = 0{\cdot}50$ respectively. Both values of m' happen to be rather greater than the corresponding $\bar{m}$, because the apparent mortalities from V to VI and from VI to VII happen to be rather higher than the average, and these ages have the overwhelming influence on the value of m'. Because of random variations, neither this fact, nor the fact that the two values of m' are more nearly equal, are very useful in evaluating the relative advantages of the two possible overall mortalities, though such comparisons over a period of years might give useful results. However, the present figures are sufficient to indicate the degree of bias of s, the percentage survival. The mean values of s over the seven ages, for each of the two pairs of years are 67·0 and 65·3, while the percentage survivals corresponding to the mean values of m are 66·5 and 64·2 respectively, indicating, as expected, a positive bias in s of about 1 per cent. Using (3.9) and estimates of the variance of the age composition, a theoretical variance of m may be calculated, and this can be compared with the observed variance. As there is little difference between the two sets of mortalities, and also because during the 3 years covered by the data the fishing on the North Sea plaice remained constant, the observed variance has been calculated from all 14 separate estimates of m. This gives an observed variance of m of 0·0266.

In Table 1.11 it was shown that by far the greatest contribution in the variance of the age-composition of the landings came from the sampling variance of the age-length key. The variance due to this in the present data can be readily calculated, and for the biological year 1952-3 gives, for the quantities ${}_1\sigma_x$ of the previous section the values 0·062, 0·089, 0·145, 0·165, 0·168, 0·155 and 0·079 for the age-groups VI to XII+ respectively. This gives a mean value of σ^2 of 0·0169. To this should be added contributions corresponding to the variance in the estimated length distribution of the landings, and in the conversion of the commercial landings to density indices, but these, particularly the former, are small. In the other two years the sampling design and intensity was the same, so that 0·0169 may be taken as representative of the variance of the age-indices in all years. Therefore, from (3.9) the predicted variance of m is 0·0169 + 0·0169 = 0·0338 compared with an observed variance of 0·0266.

From this agreement certain tentative but important conclusions may be made. Because the observed variance is not appreciably greater, and is in fact smaller, than the calculated variance, there is no reason to suppose that there is any important factor, other than those considered, affecting the age density indices, and hence the mortality estimates, differentially. This does not, of course, exclude the possibility that, say, the older ages are consistently and progressively underestimated, thus giving an artificially high mortality rate. The consistency in one year's mortality for different ages does mean that the sampling for age is consistent between any pair of years, while the consistency in mortality from one year to the next shows that the indices of density used are consistent. The very good agreement between the two variances is also, of course, a check on the results of the previous, and other, sections.

SUMMARY

Part I. Analysis of samples from commercial landings

The usual sampling of commercial fish populations, aimed at estimating growth and mortality is subjected to statistical analysis, and the sources of variance and bias are examined.

For length-distribution, it is found advisable to spread a given sampling effort over many ships' catches, rather than to take larger samples from a few. Sub-divisions of sampling by months, types of gear, etc., all tend to reduce the total variance, but of those possible, the sub-division by market categories is usually the most advantageous.

Errors in age determination tend to give a description of age-distribution in which the fluctuations are damped, but the effect of moderate and regular errors on estimates of mortality is not serious.

Age-composition may be determined by sampling directly, but the use of length-distributions as an intermediate step usually gives a smaller variance.

Part II. Natural Population

The conceptions of vulnerability, aggregation, and concentration are defined. Variations in these will affect the index of density as obtained in the usual manner from catch and effort data, and where possible, methods of correcting for them are attempted.

Variations in concentration call for sub-division by areas, for which methods of treating the data are outlined. Concentration in time is also corrected by sub-division.

Differences in vulnerability may include, as well as the effect of skill, such measurable terms as the tonnage of trawlers, for which corrections may be made.

The saturation of certain fishing gears, e.g., lines, can form an important factor in the assessment of effort, and a model is proposed for expressing this effect.

Fishing effort need not be recorded *in toto*. Quite efficient estimates are obtainable by a sample census.

Part III. Population Parameters

Estimation of growth rate is straightforward ; but to obtain unbiased estimates of mortality the exponential rate should be used. The advantages of different methods of weighting depend on the circumstances. In estimates of mortality of North Sea plaice the variance is almost entirely assignable to known constituents.

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